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BIRD USE OF ARCTIC TUNDRA HABITATS AT CANNING RIVER DELTA, ALASKA

UNIVERSITY OF ALASKA M.S. 1983

BIRD USE OF ARCTIC TUNDRA HABITATS AT CANNING RIVER DELTA, ALASKA

A

THESIS

presented to the Faculty of the
University of Alaska in Partial Fulfillment
of the Requirements
for the degree of

MASTER OF SCIENCE

By

Philip D. Martin, B. A.

Fairbanks, Alaska

December, 1983

BIRD USE OF ARCTIC TUNDRA HABITATS AT

CANNING RIVER DELTA, ALASKA

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ABSTRACT

Seasonal patterns of abundance of shorebirds and Lapland Longspurs were studied at the Canning River delta. Study plots with differing habitat characteristics were examined: upland, mesic, and lowland tundra, and coastal saline flats. Nesting density was greatest in the mesic plot, but the lowland received intense use by late summer transients; use of the saline habitat was consistently high. Cold weather in July, 1980 probably reduced prey availability. Aquatic habitats, especially polygon troughs, produced a high proportion of the adult insect biomass. Comparison of energetic requirements of birds with the energetic value of their prey supply suggests that food could have limited reproductive success. Availability of both aquatic and terrestrial insects may contribute to high breeding bird density in structurally diverse habitats. Heavy use of wet/flooded tundra by late summer migrants probably reflects abundance of midge (Diptera: chironomidae) larvae in pond sediments.

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INTRODUCTION

The coastal plain of the Arctic National Wildlife Refuge has been identified as an area with potential for significant reserves of oil and gas (U. S. Fish and Wildlife Service, 1983). The Alaska National Interest Lands Conservation Act of 1980 mandated oil and gas exploration on most of the coastal plain of the refuge, with a full report on the prospects for petroleum development due to Congress by 1986. In response to the need for baseline information on bird populations, the U. S. Fish and Wildlife Service supported this bird population study at the Canning River delta in 1979 and 1980 with the following objectives:

1. Estimate avian populations in the major coastal tundra habitat types according to the species and according to the entire community, during two successive breeding seasons, including the periods of spring and fall migration.
2. Determine the extent of bird utilization of the coastal lagoons and estuaries of the Canning River delta.
3. Determine the preferred breeding habitats of birds nesting in arctic coastal tundra of the Canning River delta.
4. Evaluate the relationship of productivity of the major avian habitats to use by breeding birds on the arctic coastal plain.

5. Identify habitats that are of critical importance to birds using the Canning River delta.

A summary of this study was presented by Martin and Moitoret (1981), and a detailed consideration of bird use of coastal lagoons and estuaries was reported by Moitoret (1983). A detailed treatment of bird distribution related to tundra habitat types is presented here.

In the two seasons of field work at Canning River delta, 84 species of birds were observed (Table 1). Of these, 31 species were confirmed breeders. Many of these, including the loons, waterfowl, larids, and several shorebirds, nested in low densities and/or in uncommon habitats. At Canning River delta there were seven species that were common and widely distributed breeders: Lesser Golden-Plover, Semipalmated Sandpiper, Dunlin, Buff-breasted Sandpiper, Red-necked Phalarope, Red Phalarope, and Lapland Longspur. With the exception of the longspur, these are all "shorebirds," i.e. members of the families Charadriidae and Scolopacidae. These seven species, along with several other shorebirds (most notably Black-bellied Plover and Long-billed Dowitcher) that were not common breeders but were fairly common as migrants, constitute the assemblage of species with which this study is concerned.

Details of status and phenology for all bird species were presented in Martin and Moitoret (1981). Most tundra birds arrive very soon after habitat becomes available, following snow melt in late May. Although timing of nest initiation varies with the particular year and species, the nesting period generally begins in the second and third week of June, one to two weeks after the birds' arrival. Incubation periods

Table 1. Bird species recorded at Canning River delta, 1979-1980. Sequence and nomenclature follow A.O.U. (1982). Asterisk (*) denotes confirmed breeding species in the study area.

*Red-throated Loon	Gavia stellata
*Arctic Loon	Gavia arctica
Yellow-billed Loon	Gavia adamsii
*Tundra Swan	Cygnus columbianus
Greater White-fronted Goose	Anser albifrons
Snow Goose	Chen caerulescens
Ross' Goose	Chen rossii
*Brant	Branta bernicla
*Canada Goose	Branta canadensis
Green-winged Teal	Anas crecca
Mallard	Anas platyrhynchos
*Northern Pintail	Anas acuta
Northern Shoveler	Anas clypeata
Gadwall	Anas strepera
American Wigeon	Anas americana
Greater Scaup	Aythya marila
*Common Eider	Somateria mollissima
*King Eider	Somateria spectabilis
*Spectacled Eider	Somateria fischeri
*Oldsquaw	Clangula hyemalis
Black Scoter	Melanitta nigra
Surf Scoter	Melanitta perspicillata
White-winged Scoter	Melanitta fusca
Red-breasted Merganser	Mergus serrator
Northern Harrier	Circus cyaneus
Rough-legged Hawk	Buteo lagopus
American Kestrel	Falco sparverius
Peregrine Falcon	Falco peregrinus
Gyrfalcon	Falco rusticolus
Willow Ptarmigan	Lagopus lagopus
*Rock Ptarmigan	Lagopus mutus
Sandhill Crane	Grus canadensis
*Black-bellied Plover	Pluvialis squatarola
*Lesser Golden-Plover	Pluvialis dominica
Whimbrel	Numenius phaeopus
Hudsonian Godwit	Limosa haemastica
Bar-tailed Godwit	Limosa lapponica
*Ruddy Turnstone	Arenaria interpres
Red Knot	Calidris canutus
Sanderling	Calidris alba
*Semipalmated Sandpiper	Calidris pusilla
Western Sandpiper	Calidris mauri
White-rumped Sandpiper	Calidris fuscicollis
*Baird's Sandpiper	Calidris bairdii
*Pectoral Sandpiper	Calidris melanotos

Table 1. (cont).

*Dunlin	Calidris alpina
*Stilt Sandpiper	Calidris himantopus
*Buff-breasted Sandpiper	Tryngites subruficollis
*Long-billed Dowitcher	Limnodromus scolopaceus
Common Snipe	Gallinago gallinago
*Red-necked Phalarope	Phalaropus lobatus
*Red Phalarope	Phalaropus fulicaria
Pomarine Jaeger	Stercorarius pomarinus
*Parasitic Jaeger	Stercorarius parasiticus
Long-tailed Jaeger	Stercorarius longicaudus
Herring/Thayer's Gull	Larus argentatus/thayeri
*Glaucous Gull	Larus hyperboreus
Black-legged Kittiwake	Rissa tridactyla
*Sabine's Gull	Xema sabini
*Arctic Tern	Sterna paradisaea
(Thick-billed ?) Murre	Uria sp.
*Black Guillemot	Cepphus grylle
Horned Puffin	Fratercula corniculata
Snowy Owl	Nyctea scandiaca
Short-eared Owl	Asio flammeus
unid. flycatcher	Empidonax sp.
Horned Lark	Eremophila alpestris
Cliff Swallow	Hirundo pyrrhonota
Common Raven	Corvus corax
Gray-cheeked Thrush	Catharus minimus
Varied Thrush	Ixoreus naevius
Yellow Wagtail	Motacilla flava
Water Pipit	Anthus spinoletta
Orange-crowned Warbler	Vermivora celata
Yellow Warbler	Dendroica petechia
American Tree Sparrow	Spizella arborea
Savannah Sparrow	Passerculus sandwichensis
White-throated Sparrow	Zonotrichia albicollis
White-crowned Sparrow	Zonotrichia leucophrys
Dark-eyed Junco	Junco hyemalis
*Lapland Longspur	Calcarius lapponicus
*Snow Bunting	Plectrophenax nivalis
Rusty Blackbird	Euphagus carolinus
*Common/Hoary Redpoll	Carduelis flammea/hornemannii

range from 12 days for the Lapland Longspur to 26 days for the Lesser Golden-Plover. Lapland Longspur young are altricial, remaining in the nest for about eight days; in contrast, young shorebirds are precocial and leave the nest within a day of hatching. Peak hatching for longspurs is in late June to early July; for shorebirds it is in early to mid-July.

The shorebirds and the Lapland Longspur are top level consumers in the "detritus-based trophic system" of MacLean (1980). Most of what we know of the ecology and behavior of these birds comes from studies conducted at Barrow. The essential features of habitat use and trophic relations of these birds as revealed by work at Barrow were summarized by MacLean (1980); I reiterate some of the most important points below.

The best known species are the Lapland Longspur and four common members of the shorebird genus Calidris: Semipalmated Sandpiper, Baird's Sandpiper, Dunlin, and Pectoral Sandpiper. These species show considerable overlap in both diet and habitat use. The most important components of their arthropod diet are dipterans of the families Tipulidae (crane flies) and Chironomidae (midges). Lapland Longspurs differ from the shorebirds in that they feed on seeds in early June and are more dependent on Tenthredinidae (sawflies) in late summer, rather than the midge larvae prevalent in shorebird diets at that time (Custer and Pitelka, 1978). At Barrow, there are four species of crane flies, the most important of which are Tipula carinifrons, a large species found in mesic and dry sites, and Pedicia hannai, a smaller but more numerous species found in wet habitats. Both of these species have

multi-year life cycles, requiring at least four years to mature, two of which are spent in the fourth and final larval instar (MacLean, 1973; Clement, 1975). The prolonged life cycle with overlapping cohorts results in a high average biomass of crane fly larvae in the top few centimeters of soil. This food resource is extremely important to tundra birds. At Barrow, 72% of the diet of adult Lapland Longspurs from early to mid-summer, and virtually the entire June diet of adult Dunlins is made up of Tipula carinifrons. Semipalmated Sandpipers (Holmes and Pitelka, 1968), and probably Red Phalaropes (Tracy and Schamel, 1983; Butler et al., 1980), are more dependent on the aquatic midges, some of which also have multi-year life cycles (Butler, 1980).

A highly synchronized emergence of crane flies occurs in early or mid-July (MacLean and Pitelka, 1971). This coincides with the peak emergence of other dipterans, notably midges, and results in an abundance of surface-active insects during mid-July (Holmes, 1966b). The peak of hatching for shorebirds coincides with the period of peak abundance of surface-active insects. Shorebird young rely almost entirely on these insects for the first week or two after hatching (Holmes and Pitelka, 1968).

Holmes (1966a) described seasonal habitat use by Dunlins at Barrow and attributed seasonal shifts in habitat to changes in food availability. He also showed (1970) that breeding density of Dunlins was correlated with food availability. I wanted to test whether observed habitat use patterns at Canning River delta were related to food availability; based on food habits studies at Barrow, I chose to monitor

emergence of crane flies and midges as an index of the food available in various tundra microhabitats.

In 1979 I compared bird use on two contrasting sites -- upland and lowland. The contrast in bird use raised questions about the effect of heterogeneity of habitat on bird distribution. Would bird use on a site which was a mixture of upland and lowland be an "average" of the two sites, or did the heterogeneity confer some special quality on the habitat resulting in a unique pattern of bird use? A third area, the mesic plot, was added in 1980 to address this question.

Censuses in an area of salt-influenced coastal tundra (West Branch flats) were conducted as part of Moitoret's (1983) study of bird use of marine littoral habitats. The results of this census bring perspective to the rest of the tundra census data and are reported here for comparative purposes.

In summary, the census plot data were used to address a suite of related questions:

1. How does bird use differ in an upland vs. lowland tundra site with respect to breeding density and use by transients?
2. How does the interspersion of upland and lowland microhabitat patches affect bird use of an area?
3. Does the differential availability of food resources in various microhabitats, as represented by crane fly and midge emergence, correspond to differences in bird use observed between study plots?

4. How does use of saline coastal tundra differ from "inland" tundra areas?

STUDY AREA

Location

The study area was located in the vicinity of Brownlow Point (70° 10'N, 145° 50'W), approximately 85 km west of the village of Kaktovik (on Barter Island) and 95 km east of Prudhoe Bay (Fig. 1). The Brownlow Point vicinity is shown on 1:63,360 USGS maps Flaxman A-3 and Flaxman A-4. Tundra study plots and other locations referenced in the text are shown in Figure 2.

Topography and Geomorphology

In the eastern portion of the Alaskan arctic slope the coastal plain is narrow; the Canning River emerges from the mountains of the Brooks Range onto the foothills only 50 km upriver from the study area. The main channel of the river swings abruptly eastward just before reaching the delta, while the Staines River and a second distributary (hereafter named the West Branch) continue northward and enter the Beaufort Sea south of Flaxman Island. The study area is located between the floodplains of these channels of the Canning River within an area designated "thaw lake plain," exhibiting "...typical coastal plain topography, with large, oriented thaw lakes, drained lake basins, and expanses of low-centered ice-wedge polygons..." (Walker et al. 1982, p. 11). This terrain is typical of the western sectors of the Alaskan arctic slope, but it is rare in the Arctic National Wildlife Refuge.

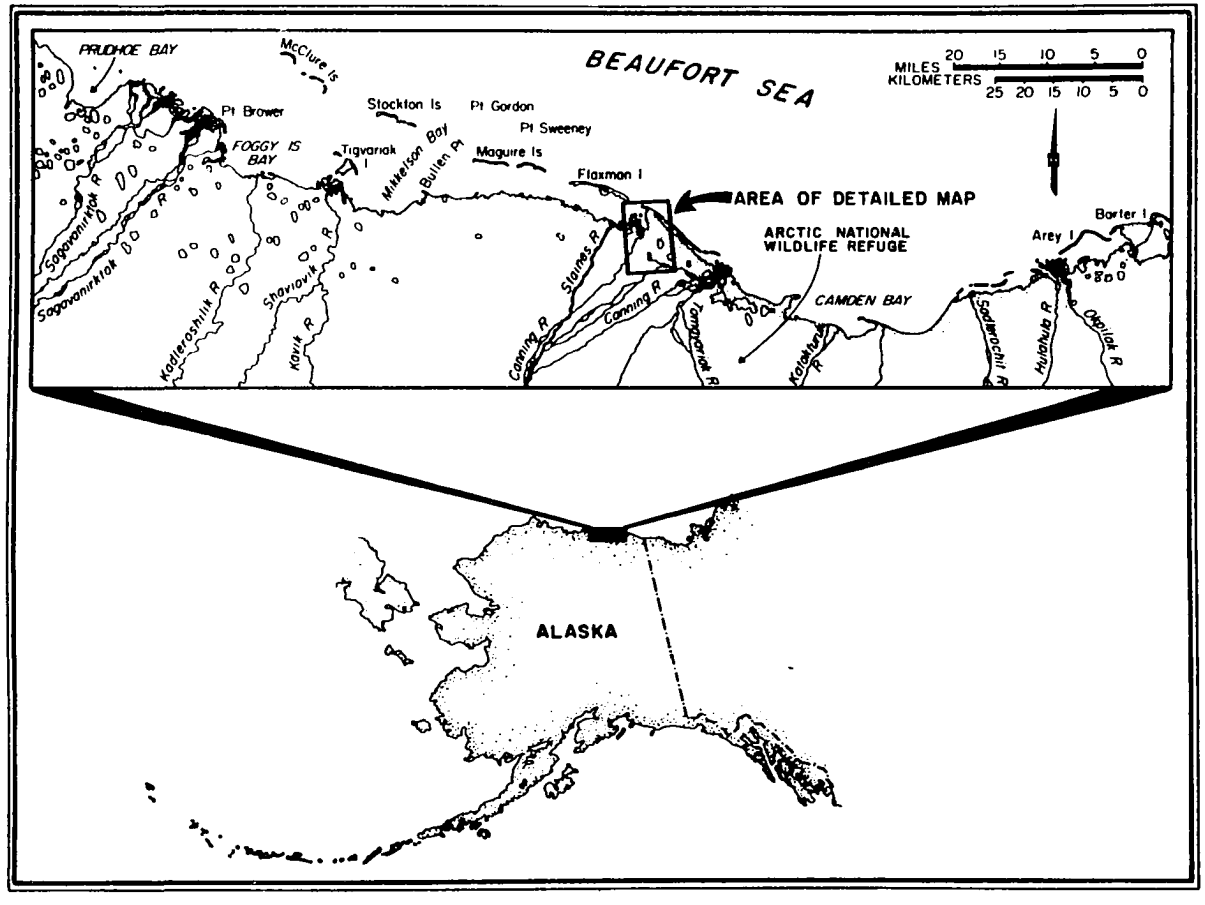


Figure 1. Location of Canning River delta study area in relation to Alaska and the Beaufort Sea coast.

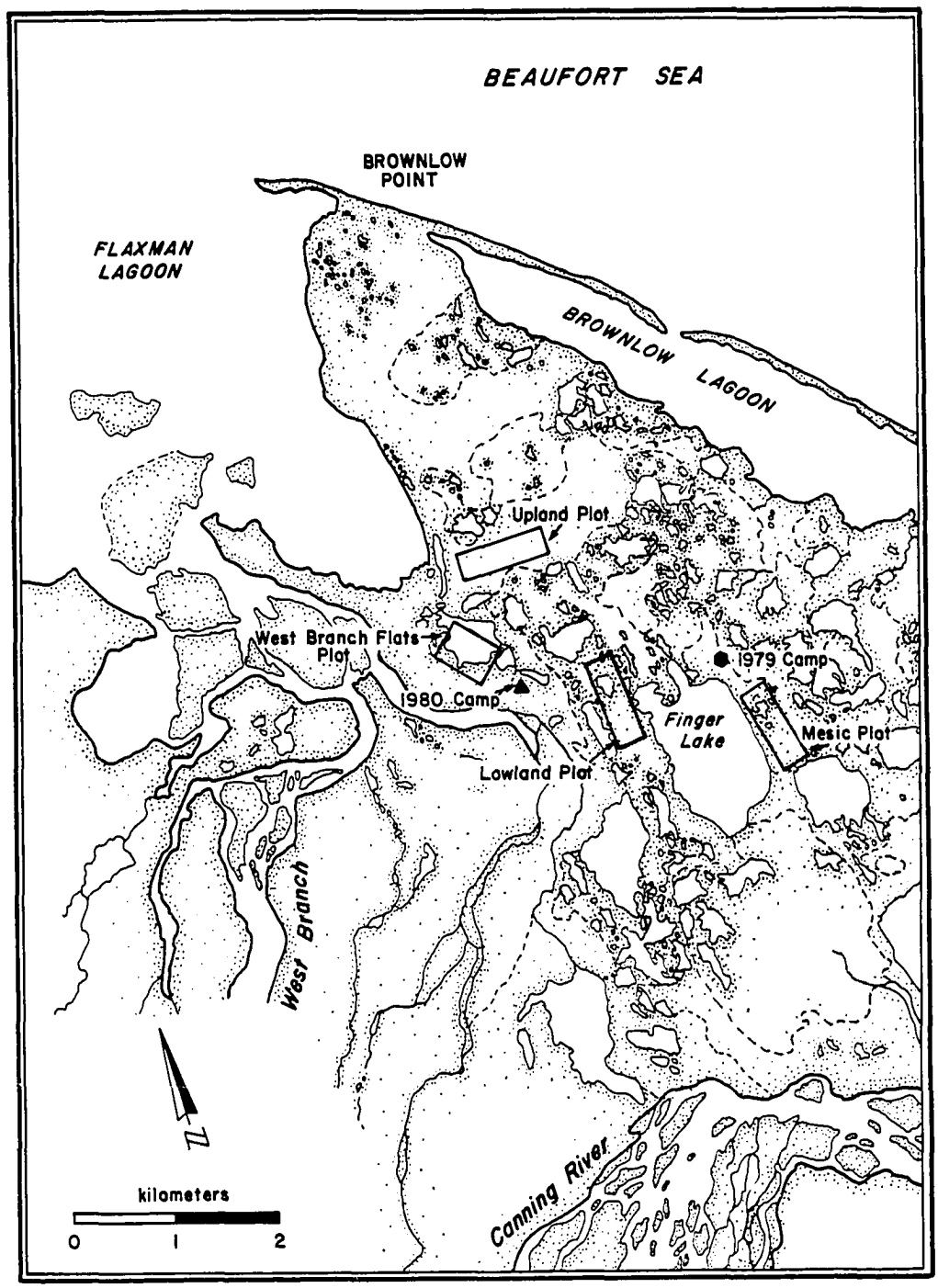


Figure 2. Detail of the Canning River delta study area showing location of camp sites and study plots. Wet and flooded tundra areas (west and north of 1980 camp only) are shaded, and enclosed in dashed lines.

The study area is underlain by a geological unit described as the "Flaxman Formation" by Leffingwell (1919). Hopkins (1978) contrasted the Flaxman Formation outcrops with the predominant arctic coastal plain surface geology:

> ...east of Oliktok Point, the Arctic Coastal Plain is underlain by a series of coalescing alluvial and glacial outwash fans extending northward from the Brooks Range...They consist mostly of sandy gravel. The alluvial fans generally extend to the coast, but in some places, the immediate coastal area is occupied by the Flaxman Formation, a marine sandy mud of Pleistocene age which contains abundant glaciated pebbles, cobbles, and boulders foreign to Alaska and quite different in lithology from the gravel of the Brooks Range origin in alluvial fans...
>
> Gravel derived from alluvium and outwash of streams draining the Brooks Range consists largely of chert, graywacke, and grit, and includes notable quantities of vein quartzite, while gravel derived from the Flaxman Formation consists largely of dolomite and also includes notable quantities of red quartz, red granite, pyroxenite and diabase.

Typical of arctic coastal plain localities, the Canning River delta is flat and its topography is dominated by patterned ground associated with permafrost. The only abrupt landscape features are those associated with the river system and the Beaufort Sea coast. Coastal "bluffs", many of them exceeding three or four meters in height, occur on the Beaufort Sea shoreline; they are particularly pronounced on the east shore of Flaxman Lagoon and also near the mouth of the Canning River. Cut banks and lakeshore bluffs 3 to 5 m in height also occur. Elevation of the study area ranges from 1.5 m to 3.5 m above sea level in lowland areas, up to 7 or 8 m above sea level on ridges associated with lakeshore bluffs. A ridge (maximum height approximately 10 m) runs east-west approximately 3.5 km south of Brownlow Point and was the location for the upland study plot.

This uniformity of terrain, however, is not indicative of biological uniformity. The microrelief features associated with permafrost, as well as the erosional features described, provide distinct drainage and soil characteristics producing an array of vegetation types. Viewed from the air, the study area has the appearance of a lattice-work due to the presence of ice-wedge polygons. The growth of subterranean ice-wedges is manifest at the surface by a pattern of polygonally shaped basins enclosed by rims and separated by troughs. Polygon troughs are often enlarged and deepened into pools by the process of thermokarst subsidence. Other permafrost landforms, such as "bird mounds," frost scars, and string-bogs also modify the local vegetation. A description of permafrost landscapes and geomorphic processes relevant to this area is contained in Walker et al. (1980).

Overlain upon the process of polygonization is the formation and eventual drainage of ponds and lakes in the "thaw lake cycle" (Britton, 1957). Over a timespan of thousands of years small impoundments of water in polygon basins coalesce to form larger ponds and lakes. Wind driven wave action and thermal erosion continue to enlarge these lakes until a divide is breached and the lake drains, leaving a marsh or a complex of ponds and marsh. The remaining lakeshore bluffs provide a special habitat type: erosion of polygons near lake shores results in formation of high-centered polygons and this well-drained terrain may remain long after lake waters have drained (Walker et al. 1980).

Climate

The Canning River delta has an arctic coastal climate, similar to that recorded by the U.S. Weather Service station at Barter Island. The Beaufort Sea is frozen most of the year, but from break-up in mid-June to mid-July through freeze-up which occurs during the period from September to November, the Beaufort Sea exerts a moderating influence over the weather of the coastal area. Compared with inland areas, the immediate coast experiences warmer autumns and cooler spring and summer temperatures. In spring and summer there is a very steep temperature gradient on the arctic coastal plain with temperatures falling off rapidly as one approaches the coast (Walker et al., 1980).

Summer temperatures at Barter Island are cool, with mean daily maxima of about 3.4° C in June, 7.5° C in July, and 6.4° C in August. Heavy fog is characteristic of the coastal area in summer and is a factor in keeping temperatures cool and stable. Fog cover is recorded on about half the days during the months of June through August at Barter Island (U.S. Dept. of Commerce, 1979). At Barter Island, summer winds are predominantly east to east-northeast and mean wind speeds are 17 to 18.5 km/hr during the summer months (U.S. Dept. of Commerce, 1979). Annual precipitation is difficult to measure on the arctic slope because much of it falls as wind-driven snow and mist and is underestimated by conventional rain gauges. Annual precipitation recorded at Barter Island is approximately 165 mm (1948-1978 average) with about 70 mm (40%) falling in the months of June through August (U.S. Dept. of Commerce, 1978).

METHODS

Bird Census

The locations of the upland and lowland plots were chosen with the aid of an aerial photograph (scale of approximately 1:33,300). Criteria for selecting these sites included sufficient size of a homogeneous habitat (judged from appearance of the photograph) and accessibility. The mesic plot was surveyed in late summer of 1979 and was chosen on the basis of ground reconnaissance.

The mesic and the upland plots measured 300 m x 850 m (25.5 ha) and the lowland measured 300 m x 900 m (27 ha). Size and shape of the plots were determined by the configuration of habitat units in the area; I attempted to maximize plot area without including disparate habitat types. All plots were surveyed using a compass and 50 m surveyor's tape and marked with surveyor's stakes in a 50 m grid pattern.

These plots were used to determine densities of shorebirds, passerines, and ptarmigan only. Other bird species seen within the plots were recorded but not included in this analysis. Censuses were conducted on each plot at five to seven day intervals from 23 June to 30 August, 1979 and 6 June to 26 August, 1980. Censuses were conducted by two to four people walking abreast down each 50 m wide "corridor" along the long axis of the plot, recording all birds seen on the ground within the plot; birds that flew over the plot were not counted in the census total. None of the species censused are generally aerial foragers. Unfledged young of the year were not included in census totals.

All bird sightings were marked on maps of the study plots and direction of flight was noted if a bird flushed to another portion of the plot. It was impossible to eliminate all duplicate sightings of birds moving around on the plot but we attempted to keep track of individual birds and flocks. Censuses took up to six hours to perform during the nesting season when we were locating nests and broods, but as little as two and a half hours during late summer when only migrants were present.

Intensive nest searches were conducted whenever observers were on the plot during the nesting season. Rope dragging to flush incubating birds from their nests was combined with a census at least once per year on each plot. Nests were marked with two wooden tongue depressors, one inserted deeply into the ground within 0.2 m of the nest, and one placed on a prominent microsite several meters away and inscribed with directions for relocating the nest. Estimated nest densities are based on nests found and are independent of the census results, which are used as a measure of total bird use of each plot. Although I originally intended to mark incubating birds in order to eliminate renesting as an added component of breeding density, this proved impractical due to time constraints. Thus, the nest densities reported may be inflated by renest attempts.

The census of the 400 m x 500 m (20 ha) West Branch flats plot was accomplished by a single observer traveling a regular route through the area. Because of the configuration of lakes and ponds, it was impossible to walk straight line routes through the area. Instead, the

censuser traversed the narrow polygon rims that wound through the area, covering essentially all the dry land areas of the plot. The census took about two hours to perform and was conducted on 12 dates on a time-available basis from 25 June to 22 August, 1980. No special effort was made to find nests on this study plot.

Habitat Description

Habitat characteristics of the upland, lowland, and mesic plots were examined to complement the description of bird use. The parameters chosen were: microrelief, wetness, vegetation, and insect abundance.

Microrelief

Average microrelief for each plot was estimated by measuring maximum vertical difference in elevation to the nearest 0.1 m within a 5 m^2 radius of each surveyor's stake on four grid lines. These data points were treated in analysis as a simple random sample. I eliminated sites that were in ponds since the variable of interest was a measure of relief of landforms. Thus, sample size varied from 69-74 points per plot.

Temperature, Snow Cover, and Wetness

Air temperature at a height of 0.5 m above the ground surface was recorded with a continuous-recording thermograph.

In 1980, snow cover and wetness in the plots were examined using transects. Five of the 300 m short axis grid lines in each plot were chosen randomly to serve as samples. Lengths of ground along this line

were classified into one of the following categories:

1. Snow- or ice-covered ground.
2. Dry -- ground does not feel wet to touch.
3. Wet -- no standing water, but ground feels wet to touch.
4. Saturated -- no standing water, area continuously vegetated, water covers boot when stepping down.
5. Flooded -- standing water, area continuously vegetated.
6. Saturated pond sediments -- no standing water, but water/mud covers boot when stepping down; little or no vegetation.
7. Shallow water -- pond water less than 3 cm in depth.
8. Medium depth water -- pond water 3 to 10 cm deep.
9. Deep water -- pond water over 10 cm deep.

Classes six and seven were combined in analysis. Lengths of transect were assigned to one of these categories and summed to yield the total for each category. Minimum length of a recorded segment was one meter, and segments were measured to the nearest 0.5 m. Mean and variance for each class were derived using the five transects in each plot as replicates. These transects were sampled five times during the summer.

In 1979, snow melt was monitored with a single 1500 m transect through lowland and mesic habitat. Presence or absence of snow was noted at points at 10 m intervals; thus, 150 points were sampled.

Vegetation

Vegetation on each plot was characterized by quadrat sampling. Seven of the 300 m short axis grid lines were chosen randomly on each plot to serve as vegetation transects. Circular quadrats 0.25 m^2 in area were placed at 10 m intervals along these transects, for a total of 217 samples per plot. The small size of the quadrats minimized the possibility of overlapping microtopographic units within one sample. For each quadrat, presence/absence data were recorded for all plant taxa listed in Table 5.

The quadrats for all plots combined were ordinated using the Detrended Correspondence Analysis (DECORANA) routine of the Cornell Ecology Program Series (Hill, 1979). This program simultaneously performs an ordination of plant taxa and of samples, using the multivariate technique of reciprocal averaging (or correspondence analysis) (Hill, 1973; Hill and Gauch, 1980). This method results in a mutually dependent ordination of samples based on their floristics, and of plant taxa based on their distribution within samples. For presence-absence data, each sample score is equal to the mean of the scores of species contained within the sample, and each species score is equal to the mean of the scores of samples in which the species occurs. An important feature of DECORANA is that it preserves ecological distance along the entire axis. Thus, sample pairs with equivalent plant compositional differences have equivalent score differences regardless of their position on the axis. I included only taxa that I was confident of identifying in all phenological stages present in the field; samples in ponds with no vegetation were dropped from the analysis.

Insects

Sampling sites were established within the three bird study plots in both terrestrial and shallow aquatic microhabitats in 1980. Terrestrial traps were constructed from two sheets of aluminum fastened together to form a cylinder 0.25 m high and 0.50 m in diameter, thus enclosing an area of 0.20 m^2 (Fig. 3). These were inserted into the soil and covered with mosquito netting held on with elastic. In order to check the traps, the covers were removed, the ground and vegetation was carefully examined, and any adult tipulids that emerged since the last visit were captured and preserved. Nearly all specimens were captured on the ground or vegetation rather than on the trap wall or mesh cover. All specimens were preserved in formalin in the field and later transferred to 80% ethanol. Four terrestrial sampling strata were recognized: wet, mesic, dry, and mesic/frost scar. These types were not all represented in each bird study plot (Table 2). Five replicate sites were chosen randomly from each stratum sampled in each bird study plot, with each site containing a cluster of four traps. A total of 160 traps was installed 27-30 June, enclosing an area of 32 m^2. These were checked on alternate days until 29 July (after more than ten days with no appreciable emergence).

Shallow water habitats were sampled by means of a pyramid-shaped emergence trap modified after Mundie (1971) enclosing an area of 0.20 m^2 (Fig. 3). Since insects emerging from aquatic environments are phototactic they generally rise to the apex of the pyramid, where a collecting jar is located. Traps were placed with their base touching the

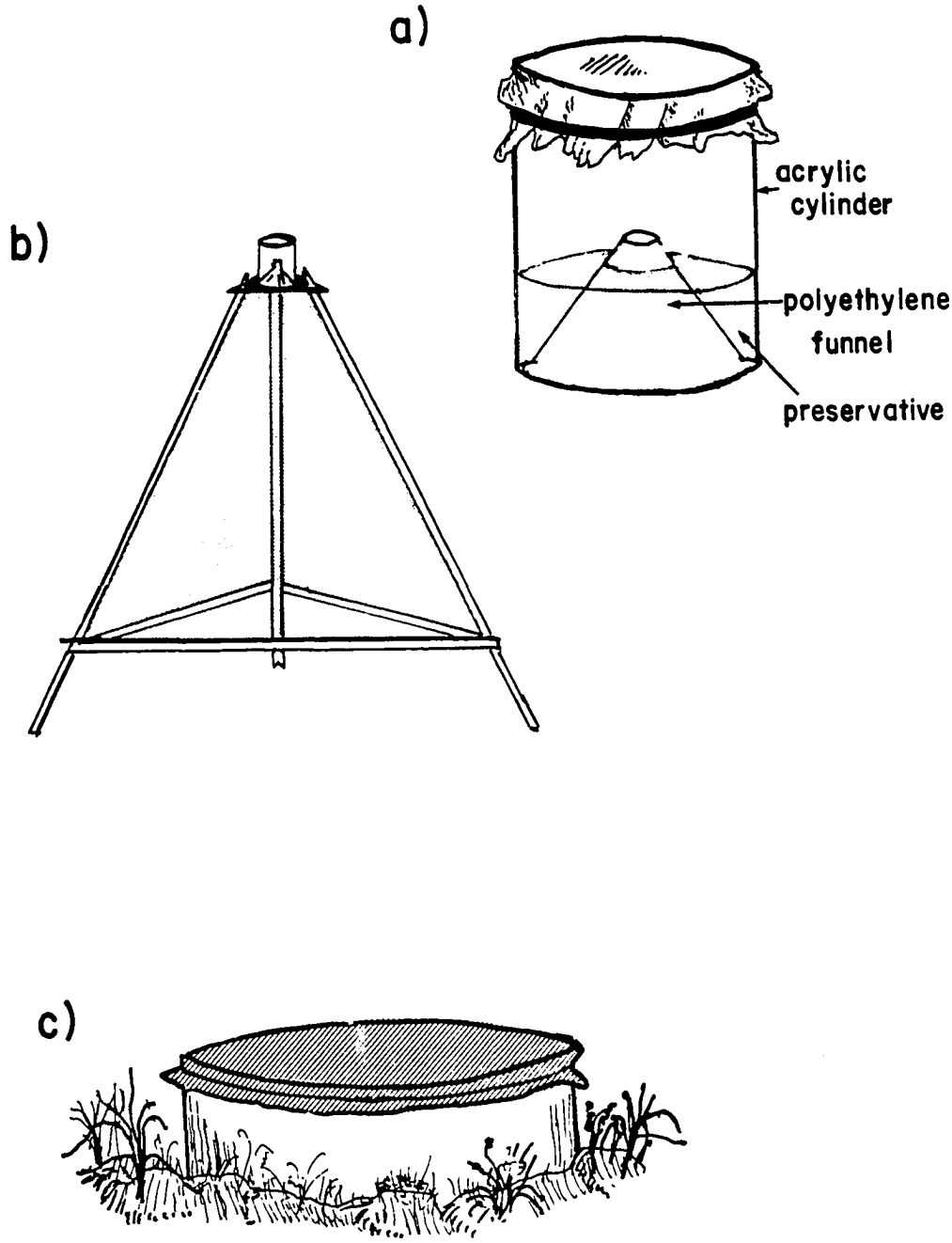


Figure 3. Insect emergence traps used at Canning River delta. Detail of collecting jar (a) placed at apex of trap used in shallow aquatic microhabitats (b) and trap used in terrestrial microhabitats (c).

Table 2. Allocation of insect emergence trap sampling effort by plot and habitat strata; dash indicates no traps.

	Upland	Mesic	Lowland
Terrestrial Traps			
wet	--	x	x
mesic	x	x	x
mesic/frost scar	x	--	--
dry	x	x	--
Aquatic Traps			
polygon basins	--	x	x
polygon troughs	x	x	x

sediments to prevent passage of swimming insect larvae or pupae. Traps were located within the zone of emergent aquatic vegetation (primarily Carex aquatilus and Eriophorum angustifolium) on the edge of both troughs and basins of ice wedge polygons, except in the upland plot, where only trough ponds were present. Five replicates were established per habitat in each study plot, for a total of 25 traps enclosing an area of 5 m^2. Traps were checked and insects removed every second or third day from 1 July to 15 August.

Once in the field, some of the seals for the collecting jars of the aquatic traps did not remain intact and formalin leaked out of the trap; these traps were dismantled temporarily for repairs. In addition, two samples were lost due to shipping damage to the storage vials. Thus, there are gaps in the data amounting to 25 out of 460 trap-days (5%) from the lowland and 30 out of 440 trap-days (7%) in the mesic plot. No traps malfunctioned in the upland plot. In order to compare emergence among the study plots and pond types sampled with unequal intensity, the total catch was standardized using mean daily emergence rather than total emergence from a trap. Using these data to estimate total emerged biomass for the season assumes that the missing emergence data would not have altered the mean significantly.

Dry weights of aquatic specimens were obtained by drying the insects at 30° C for four to five days (after which no further weight loss was detected) and weighing them on a Cahn Electrobalance to the nearest 0.01 mg. Weights for tipulids and other insects from the terrestrial traps were based on a representative sample from this study or values from MacLean and Ayres (1982).

RESULTS

Habitat Description

Temperatures, Snow Melt, and Surface Water

Maximum and minimum daily temperatures are shown in Figure 4. Using weather records from Barter Island for comparison, May temperatures were well above average in 1979, resulting in an early melt-off. Snow cover was diminished to 70% by 27 May, ice was "candled" on small ponds by 28 May, and by 1 June snow was essentially gone and standing water was abundant. Small ponds and lakes were substantially ice-free by 6 June. May of 1980 was colder than 1979. Snow melt did not even begin until 1 June, significant amounts of open water were not present on the tundra until 5 June, and small ponds and lakes were not open until 10 June. Although other factors such as the volume of the accumulated snow pack undoubtedly influence phenology of snow melt, a comparison of the two years illustrates the effect of spring temperatures on timing of snow melt and availability of habitat for birds.

Mid-summer temperatures were also very different in the two years. July 1979 was the fourth warmest in 30 years of records at Barter Island. In contrast, July 1980 was the second coldest on record. Thermograph records at Canning River delta for the first three weeks of July (a total of 504 hours) showed that temperatures exceeded 5° C for only 40 hours in 1980, but for 400 hours during this period in 1979. In 1980, temperatures fell below freezing on 6-8 July and 19-21 July; no freezing temperatures were experienced in July, 1979.

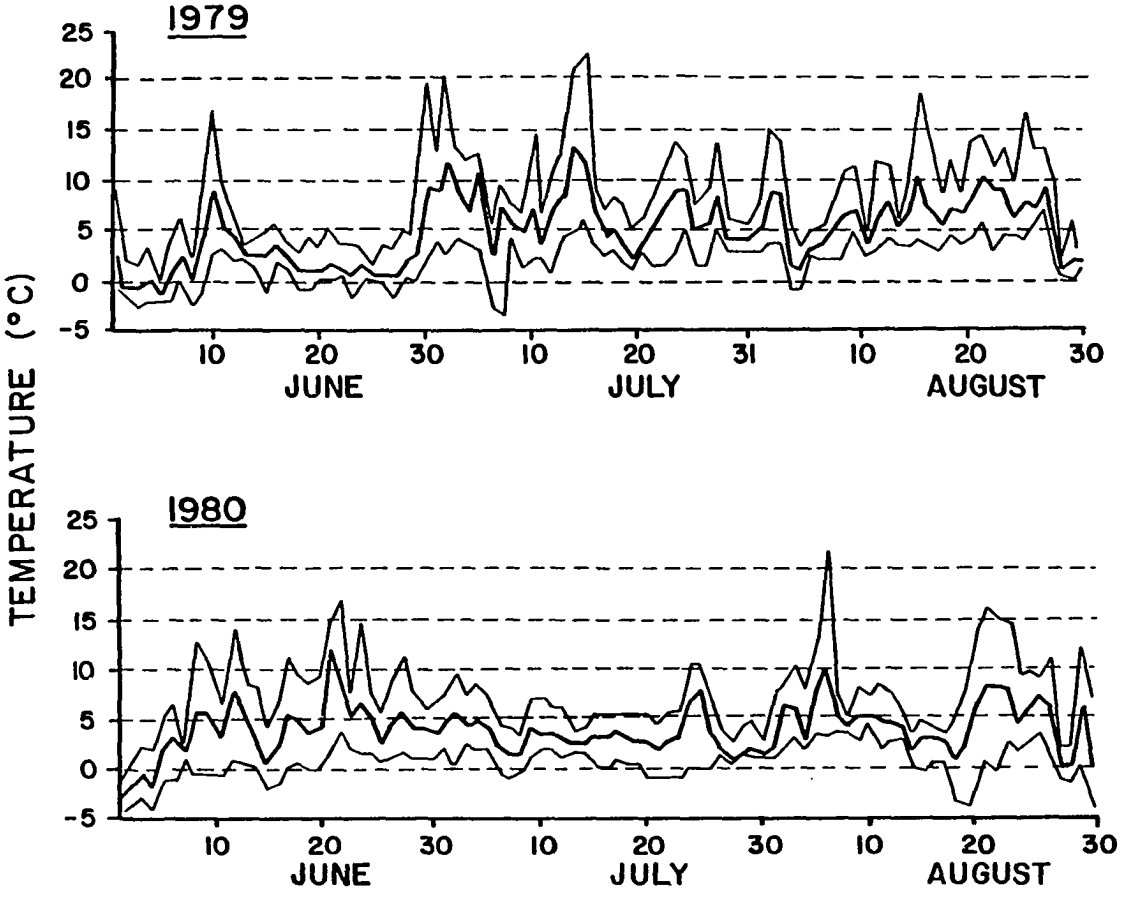


Figure 4. Daily mean (heavy line), maximum (upper line), and minimum (lower line) temperatures at Canning River delta, summer of 1979 and 1980.

Phenology of snow melt varied among study plots and between years (Fig. 5). In 1979, after a mild May, melt-off was 50% complete by 29 May and essentially complete by 1 June. In 1980, melt-off was just 50% complete on 5 June in habitats similar to the 1979 sample, and wasn't complete until 16-17 June. Table 3 shows the results of Kruskal-Wallis tests for differences in snow cover between plots in three sets of samples taken during the period of snow melt in 1980. There was a significant difference in snow cover on the first two sample dates, but by 14-17 June snow was nearly gone from all the plots and no significant difference in snow cover was found. Multiple comparisons tests (Conover, 1980) show that for 30 May-3 June, the lowland plot had the most snow cover ($p < 0.05$) and the other two plots had equivalent snow cover. On 6-9 June, the upland had less snow cover than the other two plots ($p < 0.05$). These results confirm the trends shown in Figure 5. Snow melt on the upland plot and mesic plot began earlier than on the lowland plot. Initially, snow melt advanced more rapidly on the mesic plot than the lowland because the more pronounced microrelief of the mesic plot promoted early melt of exposed microsites with southern exposures. However, the deeply incised troughs of the mesic plot retained snow longer than the lowland plot, where water collecting in the poorly drained area hastened the process of snow melt. The within-year differences in melt phenology among habitats are small compared with the between-year difference.

Following snow melt, extent of flooding can be a major factor determining availability of habitat for birds. A comparison of the

Table 3. Results of Kruskal-Wallis tests for equality of snow cover on the three study plots.

Sampling Date	Kruskal-Wallis T (d.f.)	Probability
30 May - 3 June	6.42 (2)	0.04
6 June - 9 June	8.78 (2)	0.01
14 June - 17 June	0.25 (2)	0.88

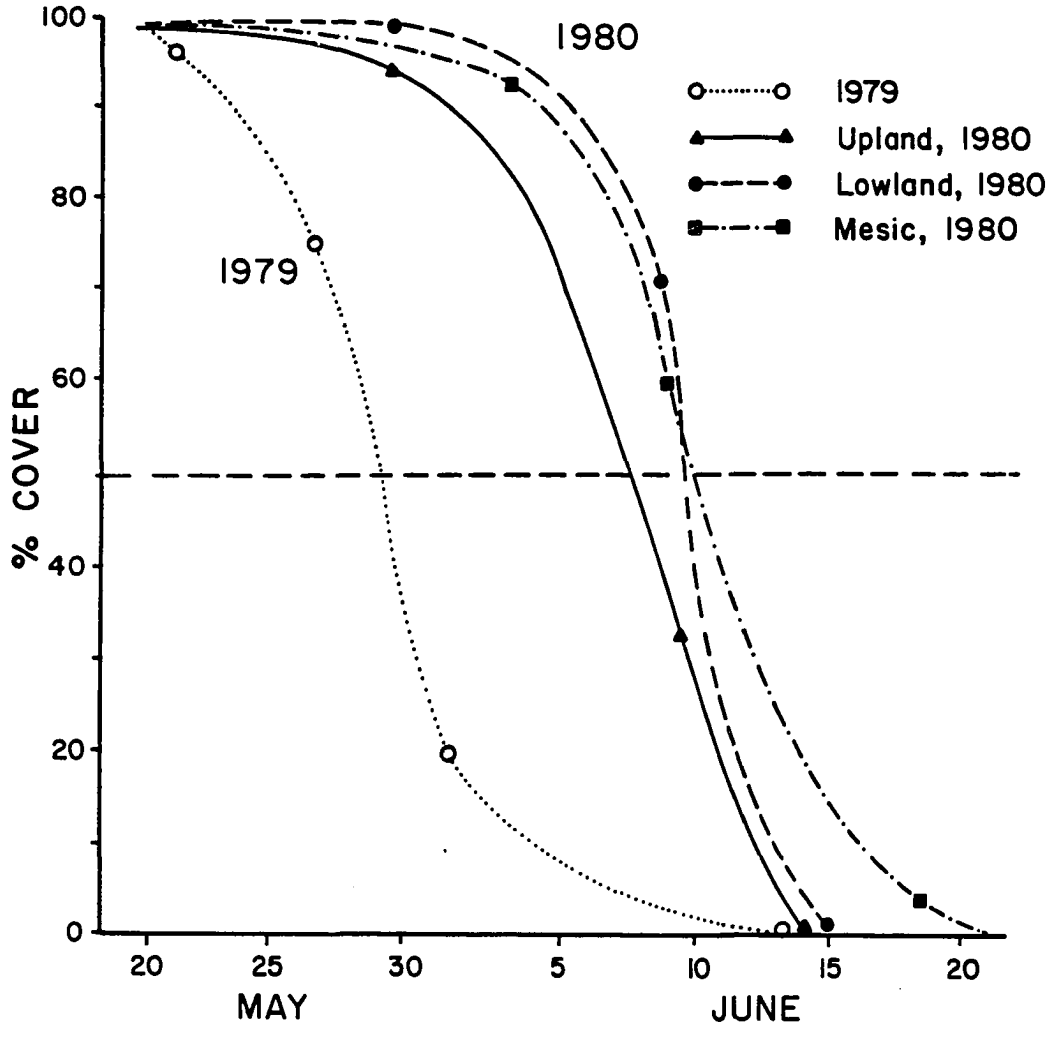


Figure 5. Snow melt recorded on the snow transect in 1979, and on three intensive study plots in 1980, at Canning River delta.

study plots with respect to ground moisture and surface water is presented in Figure 6. The lowland was wettest in mid-June, when over 70% consisted of deep water or flooded tundra, hence unavailable for bird use, compared with 20% on the upland plot and 28% on the mesic plot. By mid-July, the distribution of the wetness classes shifted, with deep water and flooded tundra greatly diminished even in the lowland. The lowland still contrasted with the other plots in its extensive areas of shallow water and exposed pond sediments. In August, cool and rainy weather resulted in re-flooding of low areas. This change was most pronounced on the lowland, where the combined proportion of moderate to deep water and flooded tundra increased from 11% in July to 57% in August. The relative increase in these categories was of similar magnitude on the upland, but involved only 11% of the area, while a three-fold increase on the mesic plot increased the proportion of these classes to 15%. Mean water depths on areas classified as "flooded" were not recorded, but it was my impression that flooded areas on the upland tended to be very shallow.

Microrelief

Mean microrelief for each of the plots is given in Table 4. Mean microrelief differed significantly among plots (Kruskal-Wallis $T=84$, $p < 0.001$). Based on a multiple comparisons test (Conover, 1971) microrelief differed among all three plots ($p < 0.001$). Mean microrelief was least on the lowland plot and variance was least there as well. The mesic plot had the greatest mean microrelief, while the upland plot had intermediate mean microrelief and highest variance, reflecting the presence of isolated mounds in an otherwise flat terrain.

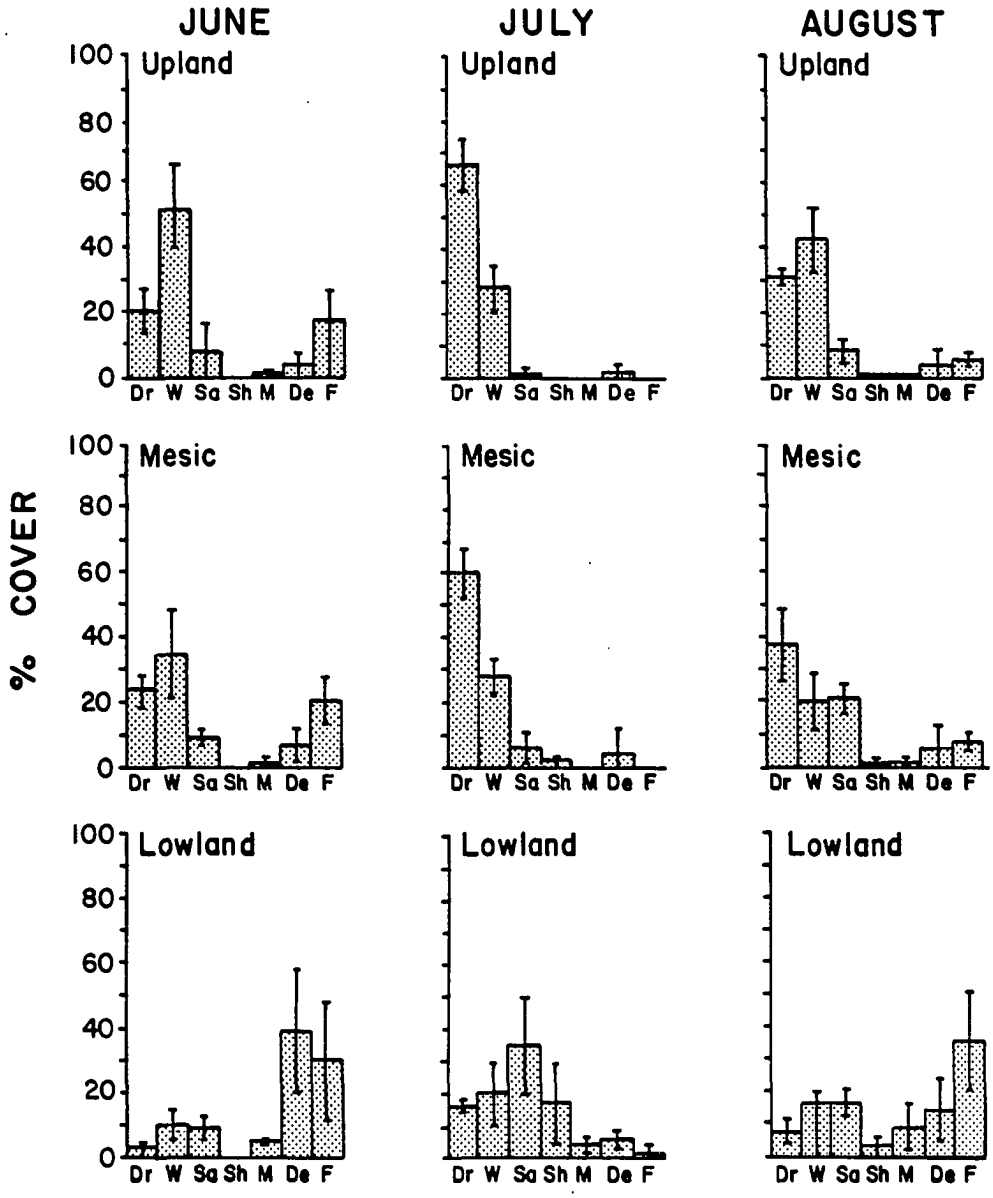


Figure 6. Distribution of samples classified by wetness on the three intensive study plots, Canning River delta, 1980. Data was derived from systematic samples taken on three occasions per plot; mean and 95% confidence interval are indicated.

Dr = dry ground
W = wet ground
Sa = saturated ground
Sh = shallow water
M = moderate depth water
De = deep water
F = flooded tundra

Table 4. Microrelief sample statistics and results of Kruskal-Wallis and Mann-Whitney tests pertaining to mean microrelief on the study plots.

Plot (sample size)	Microrelief (cm) $\bar{x}$	S.D.
Upland (72)	26.9	14.3
Mesic (69)	33.2	10.9
Lowland (74)	17.8	5.6

Ho	Probability
Upland = mesic = lowland	<0.001
Upland = mesic	<0.001
Lowland = mesic	<0.001
Upland = lowland	<0.001

Vegetation

Table 5 lists the plant taxa used in vegetation analysis and their scores on the first and second DECORANA axes. The first axis appears to represent primarily a moisture gradient, with typical hydrophiles at the upper end of the gradient and species characteristic of well-drained sites at the lower end. As an aid to interpretation of the first DECORANA axis (DA-1) I have compiled a frequency table of vegetation quadrats categorized by a priori field classification and by their DA-1 scores (with the axis divided into five equal-length segments) (Table 6). In order to conform to the design of the insect sampling program, I have separated out aquatic sites and subdivided the terrestrial sites into categories similar to the strata used for insect sampling. Mesic/frost scar samples have been divided into two classes on the basis of whether the sample was located largely on a frost scar itself or in the more heavily vegetated interstices between frost scars. Overall, the a priori classifications are consistent with an interpretation of DA-1 as a moisture gradient, but the separation of mesic and dry sites was rather poor. The proportion of samples classified primarily as "frost scar (mesic)" is significantly higher in the first segment than in the second (χ^2 contingency test, $p < 0.001$) while there is no difference in the proportion of samples classified merely as "dry", with no frost scar influence (χ^2 contingency test, $p = 0.61$). Thus, the separation of first and second segments seems to be due more to the influence of cryoturbation than to moisture. In spite of these difficulties, DA-1 is probably best interpreted as a moisture gradient.

Table 5. Plant taxa used in vegetation analysis and scores on first and second axes of DECORANA.

Species	First Axis Score	Second Axis Score
Eriophorum russeolum	470	100
Pedicularis sudetica	408	107
Carex sp.	398	-20
Juncus bigelowii	382	128
Melandrium apetalum	355	104
Cardamine pratensis	348	491
Carex membranacea	343	40
Saxifraga foliolosa	338	288
Salix ovalifolia	330	-45
Carex rariflora	318	255
Carex aquatilus	306	185
Saxifraga cernua	303	176
Saxifraga hieracifolia	279	111
Carex misandra	247	210
Eutrema edwardsii	236	-20
Polygonum viviparum	234	65
Minuartia rossii	228	185
Saxifraga hirculus	222	-39
Luzula multiflora	216	292
Salix planifolia ssp. *pulchra*	191	353
Equisetum sp.	165	-100
Salix reticulata	165	325
Salix arctica	162	21
Stellaria sp.	156	237
Saxifraga caespitosa	153	433
Eriophorum angustifolium	145	189
Luzula confusa	144	222
Cerastium sp.	107	366
Draba sp.	101	65
Pedicularis kanei/langsdorfii	101	173
Dryas integrifolia	80	113
Pyrola grandiflora	79	469
Cassiope tetragona	74	423
Peltigera sp.	74	306
Eriophorum vaginatum	73	320
Thamnolia sp.	57	170
Salix rotundifolia/phlebophylla	54	86
Dactylina sp.	51	210
Cetraria sp.	35	268
Cardamine hyperborea	30	24
Alectoria sp.	19	334
Masonhalia sp.	12	344
Silene acaulis	-31	288
Senecio atropurpureus	-43	42
Carex bigelowii	-47	-51
Chrysanthemum integrifolium	-86	55
Saxifrage oppositifolia	-112	78
Minuartia arctica	-124	147
Papaver sp.	-134	89
Astragalus umbellatus	-188	257

Table 6. Cross tabulation of vegetation samples (all plots) by *a priori* field classification and by five equal length segments of DA-1. Aquatic sites are classified separately.

a priori Class	Terrestrial DA-1 segments dry---wet 1	2	3	4	5	Aquatic Pond Edge	Pond
Dry	9	22	3	0	0	0	0
Frost scar (mesic)	32	17	1	0	0	0	0
Mesic (frost scar)	33	33	0	0	0	0	0
Mesic	14	154	69	5	0	0	0
Wet	0	13	51	83	31	52	29
Total	88	239	124	88	31	52	29

The second axis of ordination was difficult to interpret -- samples from the mesic plot were clustered at the high end of the sample ordination axis and samples from the other two plots were intermixed at the low end. The mesic plot contained a group of plant species which were virtually absent in the other two plots, and several of these appear at the high end of the species ordination axis. This group includes: Salix planifolia ssp. pulchra, Cassiope tetragona, Ledum palustre, Rubus chamaemorus, and Pyrola grandiflora. Several other taxa, such as Saxifraga foliolosa, Saxifraga caespitosa, and the lichen Peltigera aphthosa occurred with greatest frequency in the mesic plot. Without accompanying physical data, any ecological interpretation of the second DECORANA axis is speculative, but it does suggest that a major source of variation in the vegetation results from specific characteristics of the mesic plot not shared by the other two.

The sample scores from DA-1 were used as the basis for further inquiry into the spatial distribution of microhabitat types within the study plots. For these analyses, samples in standing water with no vegetation were artificially assigned a score of 400, just off the "wet end" of the scale. Table 7 shows the distribution of sample scores from each plot in five equal segments of DA-1. In order to compare the diversity of microhabitats in each plot I calculated a Shannon-Wiener diversity index score (H) according to the formula $H = -\sum_{i=1}^{n} p_i \log_e p_i$, where p(i) is the proportion of samples falling into segment i of DA-1. Since each plot has at least one sample in each segment, "microhabitat richness" is equal among plots and microhabitat diversity is equivalent

Table 7. Frequency table of vegetation samples in fifths of DA-1, Shannon-Wiener H as a measure of equitability.

	DA-1 segment					
	dry----------				----------wet	
	1	2	3	4	5	H
Upland	81	106	25	4	1	1.07
Mesic	71	99	71	26	14	1.27
Lowland	1	40	42	88	46	1.34

to equitability. The lowland has the most equitable distribution of microhabitats, followed by the mesic and upland plots, in that order (Table 7). The mesic plot had more dry area than the lowland, and more wet area than the upland, and in this sense it was a more mixed habitat than the other two. However, the mesic plot had few samples from the first segment and was dominated by samples in the "moist" second and third segments. Thus, it must be characterized as a distinct mesic microhabitat, rather than as a mosaic of habitats found in the other two plots. Therefore it provided an imperfect test of the effect of habitat heterogeneity on bird distribution.

The accessibility of microhabitats to an organism depends on the manner in which the microhabitats are interspersed, i.e. the "patchiness" of the environment. From any reference point located in a particular patch type, the probability of a second point being in the same patch type, as a function of distance (d) from the reference point, provides an index of mean patch size of the environment. This probability should approach the value of 1.0 close to the reference point and decline with distance to a value equal to the average contribution of that patch type to the plot as a whole. The rate of this decline should reflect patch size; the smaller the average patch, the more rapid the decline in this probability. I used DA-1 scores for the vegetation samples to empirically derive the probability (P) of two points being in the same patch as a function of distance, for each study plot. Aproximately 200 reference samples in each study plot were chosen at random and the DA-1 score of the vegetation at the sample point was

compared with samples at d = 10, 20, 30, 40, and 50 m. Sample pairs were defined as being in the same patch type if their DA-1 scores were within 40 units (10% of the gradient) of each other (Fig. 7), to correspond to the classification of the total sample by fifths. None of the plots show a strong relation between P and d, suggesting that the major decline in P occurs at distances less than 10 m. The predicted value of P based on a model of random spatial distribution of microhabitat types (P (null)) was determined empirically for each plot by taking a random sample (n=100) of points and determining p(i), the probability that a second point, chosen at random, would have a score within 40 units of the reference. The average of the p(i)'s is termed P(null). The relative magnitude of P(null) for the three plots corresponds to the ranking of microhabitat equitability: greater diversity of microhabitat results in lower probability that two randomly chosen points are similar. For the mesic plot P(10) is indistinguishable from P(null). For the upland plot, complete overlap of the 95% confidence intervals is reached at 20 m and for the lowland plot it is reached at 30 m. This trend indicates that the mesic plot was a finer-grained environment than the other two.

Comparison of Habitats

Contrasts in habitat characteristics that may be useful in interpreting the results of the bird sampling are presented below. Many of the differences between the plots are evident in aerial photographs (Figs. 8-10).

The greatest microtopographic relief was in the mesic plot: poly-

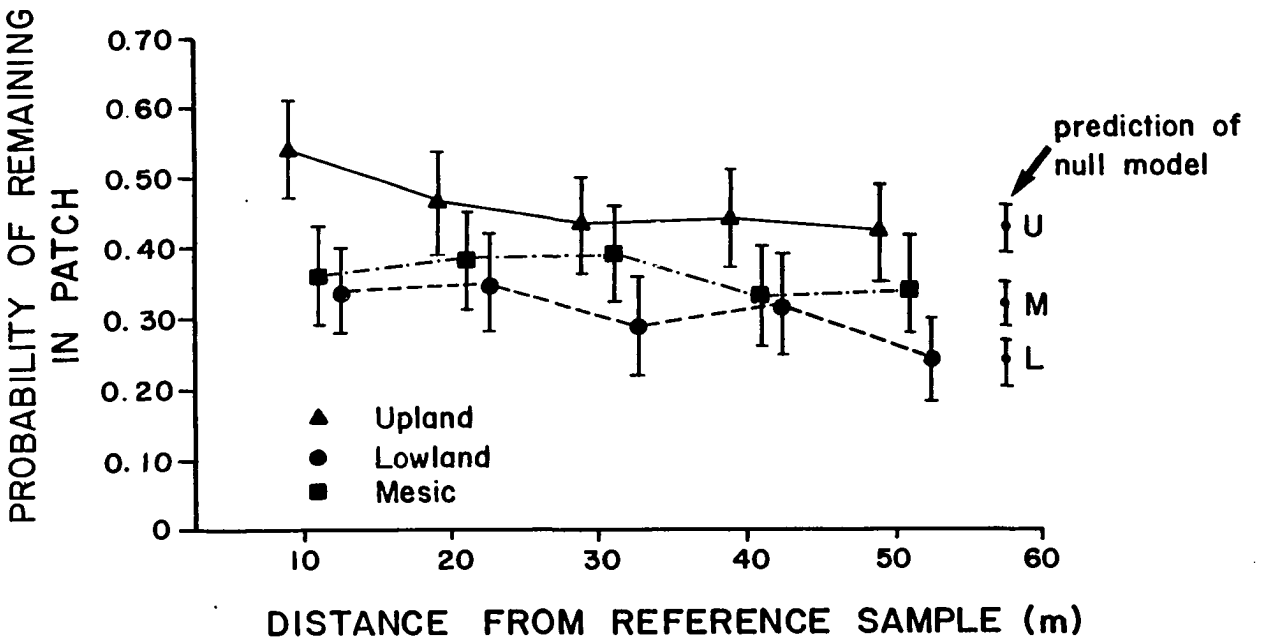


Figure 7. Probability of two points being in a similar habitat patch as a function of their proximity. Mean and 95% confidence interval shown for replicate trials at each distance.

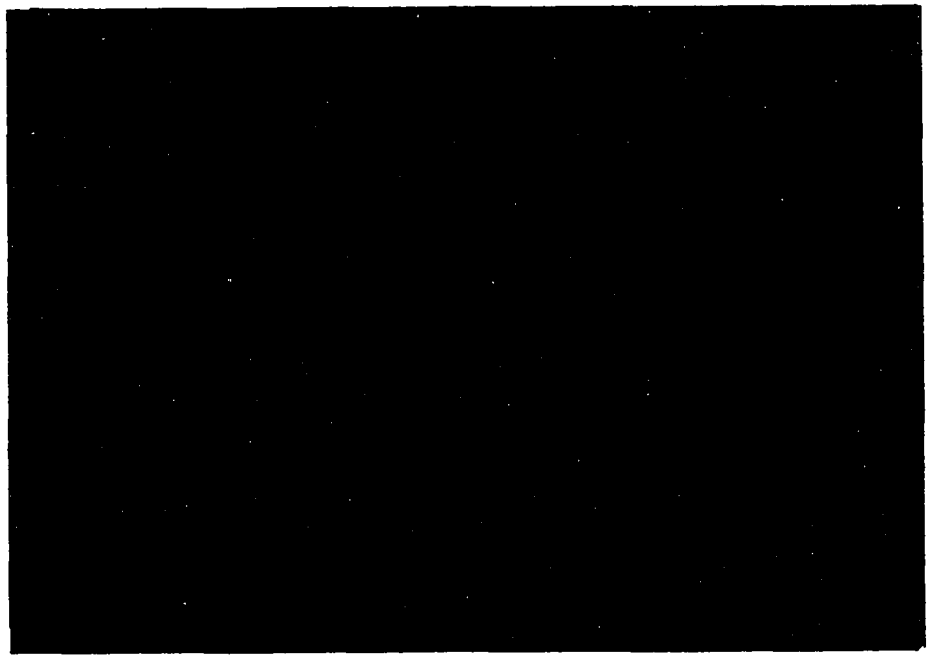


Figure 8. Oblique aerial photograph of the upland plot. A surveying stake and old vehicle tracks are visible in the lower right corner of the frame. Note the flat-topped polygons, scattered thermokarst pools, and frost scars (visible in foreground as gray circles).

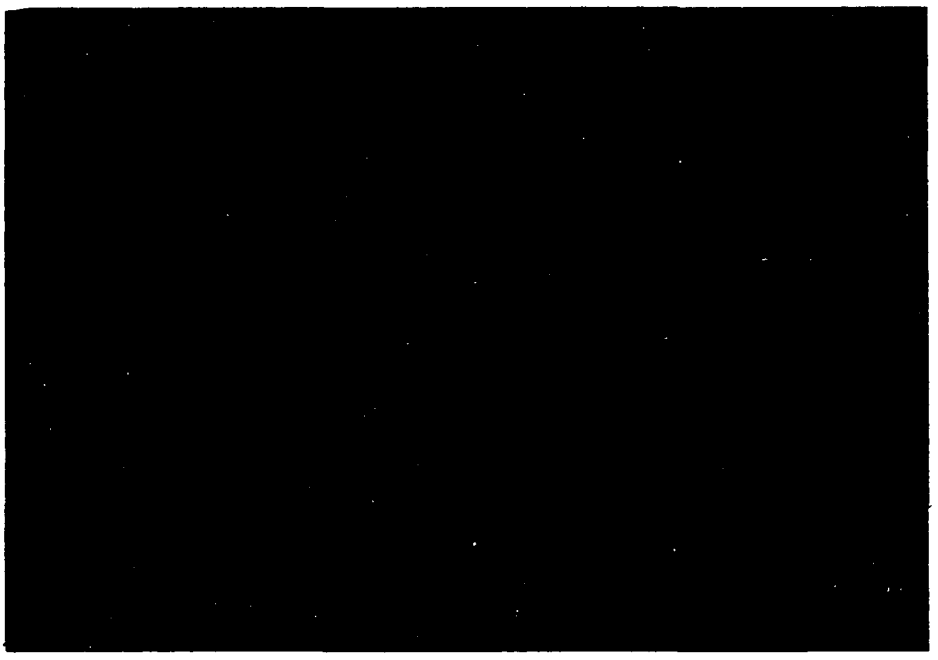


Figure 9. Oblique aerial photograph of the lowland plot. A surveying stake is visible on the pond shore in the foreground. Note the highly polygonized terrain, with low polygon centers mostly flooded, low-relief polygon rims, and troughs with standing water. Scattered thermokarst pools are present at the intersection of some troughs. Finger Lake is in the background.

Figure 10. Oblique aerial photograph of the mesic plot. The scene is a view north with the Beaufort Sea in the background; the plot extends 850 m from the foreground to the edge of the drained lake basin at the upper right. Note the numerous thermokarst pools, scattered low-center polygons, and dry polygon rims and mounds.

gon rims tended to be higher and there were high-center polygons with deeply incised troughs, probable remnants of an old lake shore. These high spots melted free of snow earlier in spring than surrounding areas, providing foraging and nest sites for birds during the first week in June.

The upland plot was the most homogeneous in terms of vegetation/habitat classes. The mesic plot, although composed mainly of moist vegetation types, contained patches of microhabitat from very wet to very dry, and was probably a finer grained mosaic of microhabitats than the other two plots. The lowland, with its many ponds, contained more of the emergent vegetation types than the other plots.

There was relatively little shallow pond edge habitat in the mesic plot; most of the ponds retained at least some water through the entire summer. During mid-summer, when the water levels receded, large areas of pond sediments were exposed in the lowland plot, but not in the mesic plot. Conversely, the lowland plot was most susceptible to flooding. It was the most inundated by spring run-off and melt water, although the other plots were at their wettest at this time also. In late summer, much of the lowland reflooded as a result of increased rainfall. The change in surface area covered by standing water was greatest in the lowland and least in the mesic plot; therefore, the mesic plot was the most predictable environment in terms of area available for feeding shorebirds. In a dry or normal year there might be much shallow water/exposed sediment for foraging shorebirds on the lowland but in a wet year this would be unavailable to shorebirds.

A Landsat environmental map (Walker et al., 1982) of the Arctic National Wildlife Refuge classified the lowland plot as a combination of pond/sedge tundra complex/aquatic tundra (Type II) and wet sedge tundra (Type III), while the mesic plot was classified mostly as moist/wet sedge tundra complex (Type IV) with a little wet sedge tundra (Type III). The upland plot is depicted on the map as Type IV, but better matches the description of moist sedge/barren tundra complex (frost-scar tundra) (Type V).

The West Branch flats plot was not sampled for physical and vegetative characteristics. The plot was located several hundred meters from the shoreline of Flaxman Lagoon, the entire area within the zone of salt water influence. The high water mark indicated by a band of driftwood completely enclosed the area and the presence of plastics and other modern refuse in the storm wrack indicated that the area had been completely inundated in the recent past. Immediately adjacent to the lagoon shoreline was a zone of saline meadow vegetated by typical halophytes, such as Puccinellia sp., Carex subspathacea, and Stellaria humifusa. Moitoret (1983) described bird use of this saline meadow habitat. The plot itself lay outside the saline meadow zone and was over 90% unvegetated, either pond water or bare sediments and organic mat. During spring flood the flats were entirely flooded by overflow from the West Branch, run-off from the adjacent tundra, and intrusion of brackish water from the bay. As summer progressed, much of the area dried out, leaving expanses of non-vegetated sediments, but some of the deeper ponds retained water through the entire season. The area was

highly polygonized, and the polygon rims were vegetated chiefly by graminoids such as Carex aquatilus and Dupontia fisheri. This is analagous to a vegetation association described by Walker et al. (1980, p.26) as present in "polygon troughs in coastal vicinity" ("Type M-8", in their classification).

Insects

Density and Biomass of Emerging Crane Flies

To analyze habitat distribution of crane flies, each insect trap was assigned a score on DA-1 based on its vegetational composition. The axis was then subdivided into five equal length segments which were interpreted as moisture classes. Numbers of crane flies emerging in 1980 were low, particularly for Tipula sp. (Table 8). Tipula specimens were collected from only eleven of 160 traps (7%). These were concentrated in dry or moist sites on the upland plot, where density was approximately 1.0/m^2 and moist sites in the mesic plot where density was 0.5-0.6/m^2. No Tipula were found in the lowland plot or in wet sites in the mesic plot. Because so few were captured, it is impossible to make any statistical inferences as to habitat preference of Tipula.

Pedicia hannai occurred in 19% of the traps, and density varied greatly between moisture regimes (Table 9). One or more Pedicia were found in 72% of traps in the wettest class while none were captured in traps classified in the driest category. The distribution of emergence (number of Pedicia emerged) was compared with an expected distribution

Table 8. Biomass (mg dry weight/m^2) of emerged *Tipula* by moisture class, as classified by DA-1, and proportion of successful traps (at least one *Tipula* captured). *Tipula* weight assumed is 12 mg/individual.

	DA-1 segments				
	dry				wet
	1	2	3	4	5
Upland					
number of traps	29	19	8	4	0
% successful	21	5	0	25	--
mg/m^2	12.36	3.12	0	15.00	--
Mesic					
number of traps	0	29	8	11	12
% successful	--	10	13	0	0
mg/m^2	--	6.21	7.56	0	0
Lowland					
number of traps	0	6	13	15	6
% successful	--	0	0	0	0
mg/m^2	--	0	0	0	0
Total					
number of traps	29	54	29	30	18
% successful	21	7	3	3	0
mg/m^2	12.36	4.44	2.07	2.00	0

Table 9. Biomass (mg dry weight/m^2) of emerged Pedicia by moisture, as classified by DA-1, and proportion of successful traps (at least one Pedicia captured). Pedicia weight assumed is 1.7 mg/individual.

	DA-1 segments				
	dry				wet
	1	2	3	4	5
Upland					
number of traps	29	19	8	4	0
% successful	0	0	12	50	--
mg/m^2	0	0	1.07	12.75	--
Mesic					
number of traps	0	29	0	11	12
% successful	--	3	0	64	67
mg/m^2	--	0.29	0	4.63	5.00
Lowland					
number of traps	0	6	13	15	6
% successful	0	17	15	27	100
mg/m^2	0	1.42	1.31	3.97	36.83
Total					
number of traps	29	54	29	30	18
% successful	0	4	10	43	72
mg/m^2	0	0.31	0.88	5.38	15.58

assuming emergence proportional to the number of traps (all plots combined) assigned to each segment (Table 10A). The null hypothesis that distribution of emerging Pedicia hannai is independent of vegetation/moisture class can be rejected (χ^2=155.7, $p < 0.001$), with preferred microhabitats at the wet end of the gradient. A finer level of resolution, dividing the gradient into tenths, reveals that the preference for wet sites falls off at the wet end of the gradient (Table 10B). Since Pedicia emergence is highly clumped, a more conservative approach is to test by frequency of occurrence in traps, rather than by actual number of Pedicia per class. The results (Table 10C) confirm the preference for wetter sites and avoidance of drier sites.

Another way of viewing habitat selection by Pedicia is by examination of its co-occurrence with plant species in the insect traps. Pairwise indices of association (Cole, 1949) were calculated between Pedicia and all plant species identified in the insect traps. Values for the index range from 1.0 (complete co-occurrence), to zero (occurring independently), to -1.0 (no co-occurrence). Significance may be tested using a χ^2 contingency table. In most cases this was precluded by low expected values, but some species showed significant positive or negative association with Pedicia (Table 11). Significant positive associations were found between Pedicia and Carex aquatilus, Saxifraga foliolosa, S. hirculus, and perhaps Polygonum viviparum. In aggregate these are species characteristic of moist areas that flood in spring but do not remain flooded throughout the season.

Table 10. χ^2 goodness of fit tests of observed Pedicia emergence against hypothesized distribution independent of moisture gradient.

A) Pedicia emergence, by number of individuals, in fifths of DA-1.

	dry 1	2	3	4	wet 5
observed	0	2	3	29	33
expected	12.0	22.7	12.0	12.7	8.1
contribution to χ^2	12.0	18.9	6.8	20.9	76.5

$\chi^2 = 135.1$, $p < 0.001$

B) Pedicia emergence, by number of individuals, in tenths of DA-1

	dry 1	2	3	4	5	6	7	8	9	wet 10
observed	0	0	1	1	1	2	19	10	28	5
expected	6.0	6.0	9.3	13.4	8.0	4.0	8.7	4.0	5.4	2.7
contribution to χ^2	6.0	6.0	7.4	11.5	6.1	1.0	12.2	9.0	94.5	2.0

$\chi^2 = 155.7$, $p < 0.001$

C) Pedicia emergence, by number of successful traps in fifths of DA-1.

	dry 1	2	3	4	wet 5
observed	0	2	3	13	13
expected	5.6	10.5	5.6	5.9	3.7
contribution to χ^2	5.6	6.9	1.2	8.5	23.4

$\chi^2 = 45.6$, $p < 0.001$

Table 11. Indices of association between Pedicia and various plant taxa, χ^2 statistic and associated probability.

	Association Index	χ^2	Probability
Carex aquatilus	0.54	5.03	<0.025
Saxifraga foliolosa	0.51	35.82	<0.001
Saxifraga hirculus	0.48	17.05	<0.001
Polygonum viviparum	0.31	3.08	<0.10
Cardamine hyperborea	-0.66	2.88	<0.10
Dryas integrifolia	-0.69	19.33	<0.001
Cetraria sp.	-0.77	14.78	<0.001
Dactylina sp.	-0.78	16.46	<0.001
Thamnolia sp.	-0.89	37.35	<0.001
Senecio atropurpureus	-0.89	10.73	<0.005
Saxifraga oppositifolia	-1.00	6.38	<0.05
Carex bigelowii	-1.00	6.05	<0.025

Timing of Crane Fly Emergence

The first adult crane flies were seen 27 and 28 June and traps were not all operating until 30 June, thus, some emergence was not quantified. Figure 11 shows cumulative emergence of Tipula and Pedicia. Median dates of emergence are 4 July for Pedicia and 9 July for Tipula. Peak emergence of Pedicia occurred 1-3 July; there was no discernable peak for the small sample of Tipula captured.

Aquatic Insect Emergence

A list of insect families collected from the aquatic emergence traps is provided in Table 12. Five groups constitute the bulk of the catch (by dry weight): large Chironomidae (greater than or equal to 4 mm in body length), Culicidae, Brachycera (mostly Muscidae, but with a few specimens from other families), Trichoptera (mostly Limnephilidae and a few Brachycentridae identified as Micrasaema scissum (G. B. Wiggins, pers. comm.)), and Nemouridae. These groups accounted for 96% of the biomass emerging from troughs and 90% of the biomass emerging from basins. The remaining specimens were small (2.0-4.0 mm) chironomids, "micronematocerans" with body length under 2.0 mm, most of which were probably chironomids, and parasitic wasps of the families Braconidae and Ichneumonidae. Insects under 2.0 mm in length are probably not important prey for birds (MacLean and Pitelka, 1971).

Kruskal-Wallis tests were performed for differences in mean daily emergence of all insects from troughs, by two-week periods, and for the entire season. For the season as a whole, the null hypothesis of equal

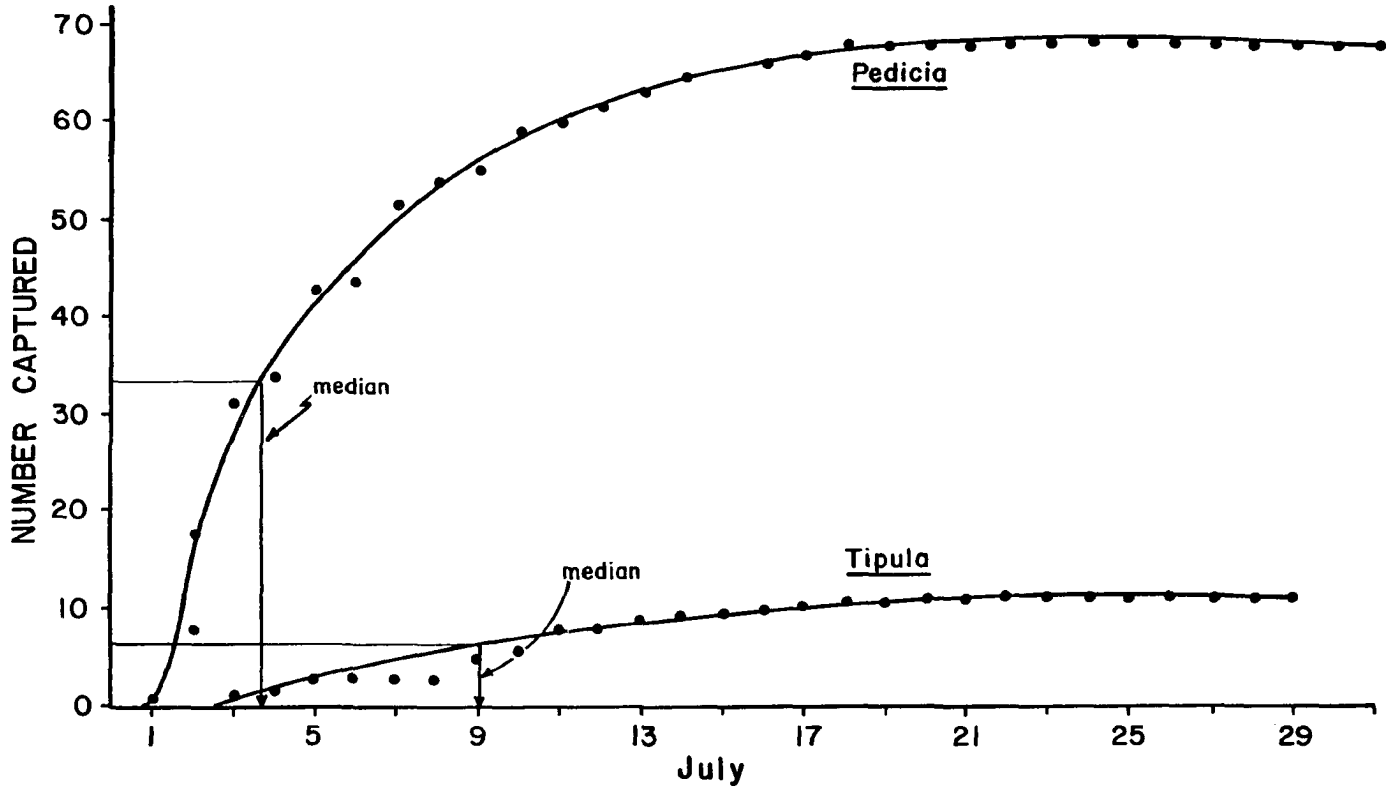


Figure 11. Cumulative emergence of crane flies, Canning River delta, 1980.

Table 12. List of insect taxa collected from aquatic emergence traps.

Plecoptera (Stoneflies)
Nemouridae
Trichoptera (Caddisflies)
Limnephilidae
Brachycentridae
Diptera (true flies)
Nematocera
Culicidae (mosquitos)
Chironomidae (midges)
Mycetophilidae (fungus gnats)
Sciaridae (dark-winged fungus gnats)
Brachycera
Ephydridae (shore flies)
Dolichopodidae (long-legged flies)
Phoridae (hump-backed flies)
Muscidae (house fly allies)
Anthomyiidae
Hymenoptera
Ichneumonidae
Braconidae

emergence from troughs in all three bird study plots is dubious (p=0.08) (Table 13). A multiple comparisons test (Conover, 1980) shows that emergence from troughs in the lowland is significantly higher than emergence in the other two plots, which are indistinguishable from each other (Table 13). A Mann-Whitney test for differences between emergence from troughs and basins reveals that emergence from troughs was significantly higher than emergence from basins in the lowland plot (Table 13), but not in the mesic plot, although mean emergence from troughs was higher than from basins. Thus, one pond type--lowland troughs--was much more productive than other types. As indicated in Table 14, most of the difference may be accounted for by midges and caddisflies.

The relative importance of these five insect groups varied among bird study plots and between pond types (Table 14, Fig. 12). Midges, which are an important food source for shorebirds at Barrow (Holmes and Pitelka, 1968), were most abundant from polygon troughs in the lowland and upland. Troughs in the mesic plot, and all basins, produced much less adult midge biomass.

Timing of Aquatic Emergence

The timing of emergence from aquatic habitats is depicted in Figure 13. While emergence was moderate in the upland in early July, it remained at very low levels on the lowland and mesic plots at this time. A pronounced spike in emergence occurred on 24 July in all three bird study plots, as temperatures warmed. This pulse in emergence, recorded over three-day periods, accounted for 50% (upland), 64% (lowland), and

Table 13. Results of Kruskal-Wallis and Mann-Whitney tests of hypotheses pertaining to aquatic insect emergence.

Ho: Upland trough emergence = lowland trough emergence = mesic trough emergence	
Time period	Probability
1-15 July	0.270
16-31 July	0.112
1-15 August	0.318
Seasonal total	0.080
Multiple comparisons for seasonal total:	
Habitats	Probability
lowland vs. mesic	0.028
lowland vs. upland	0.073
upland vs. mesic	>0.50

Ho: Trough emergence = basin emergence	
Time period/habitat	Probability
Lowland	
1-15 July	0.753
16-31 July	0.016
1-15 August	0.602
Seasonal total	0.047
Mesic	
1-15 July	0.834
16-31 July	0.076
1-15 August	0.916
Seasonal total	0.347

Ho: Upland basin emergence = lowland basin emergence = mesic basin emergence	
Time period	Probability
1-15 July	0.675
16-31 July	0.834
1-15 August	0.347
Seasonal total	0.530

Table 14. Biomass (mg dry wt./m^2) of emerged aquatic insects, by period and taxonomic group (% of total catch represented by each group is in parentheses), and by habitat (tr = polygon trough; ba = polygon basin).

	Large Chironomidae		Culicidae		Brachycera		Trichoptera		Nemouridae		*Other*		*Total*	
	tr	ba	tr	ba	tr	ba	tr	ba	tr	ba	tr	ba	tr	ba
Upland														
1-15 JL	15.18	--	0.00	--	0.44	--	1.75	--	13.70	--	1.14	--	32.21	--
	(47)		(0)		(1)		(5)		(43)		(4)			
16 -31 JL	20.75	--	11.47	--	2.91	--	19.27	--	1.04	--	2.32	--	57.76	--
	(36)		(20)		(5)		(33)		(02)		(4)			
1-15 AU	2.05	--	3.23	--	0.00	--	7.36	--	0.00	--	3.32	--	15.96	--
	(13)		(20)		(0)		(46)		(0)		(.21)			
Total	37.98	--	14.70	--	3.35	--	28.38	--	14.74	--	6.78	--	105.93	--
	(36)		(114)		(3)		(27)		(14)		(6)			
Mesic														
1-15 JL	0.00	2.40	3.26	0.84	4.04	2.34	0.00	4.60	2.47	1.31	0.00	0.00	9.77	11.49
	(0)	(21)	(33)	(7)	(4)	(20)	(0)	(40)	(25)	(11)	(0)	(0)		
16-31 JL	4.94	0.97	26.98	0.92	6.85	5.55	8.08	6.96	0.00	4.96	0.36	0.83	47.21	20.19
	(10)	(5)	(57)	(5)	(14)	(27)	(17)	(34)	(0)	(25)	(1)	(4)		
1-15 AU	1.47	1.30	1.49	0.00	2.97	6.41	2.07	1.55	0.00	0.00	3.65	4.02	11.65	13.28
	(13)	(10)	(13)	(0)	(25)	(48)	(17)	(12)	(0)	(0)	(31)	(30)		
Total	6.41	4.67	31.73	1.76	13.86	14.30	10.15	13.11	2.47	6.27	4.01	4.85	68.63	44.96
	(9)	(10)	(46)	(4)	(20)	(32)	(15)	(29)	(4)	(14)	(6)	(11)		
Lowland														
1-15 JL	12.81	2.48	0.68	2.72	0.44	2.36	2.44	2.82	0.00	6.97	0.07	0.08	16.44	17.43
	(78)	(1)	(4)	(16)	(3)	(14)	(15)	(16)	(0)	(40)	(0)	(0)		
16-31 JL	70.61	0.04	13.78	.70	9.35	8.85	8.50	4.58	0.00	3.50	1.01	1.48	103.25	20.15
	(68)	(0)	(13)	(8)	(9)	(44)	(8)	(23)	(0)	(17)	(0)	(7)		
1-15 AU	15.56	0.00	15.44	0.00	1.14	1.43	33.28	20.60	0.00	0.00	1.94	3.7	67.36	25.73
	(23)	(0)	(23)	(0)	(2)	(6)	(49)	(80)	(0)	(0)	(3)	(14)		
Total	98.98	2.52	29.90	4.42	10.93	12.64	44.22	28.00	0.00	10.47	3.02	5.26	187.06	63.31
	(53)	(4)	(16)	(7)	(6)	(20)	(24)	(30)	(0)	(17)	(2)	(8)		

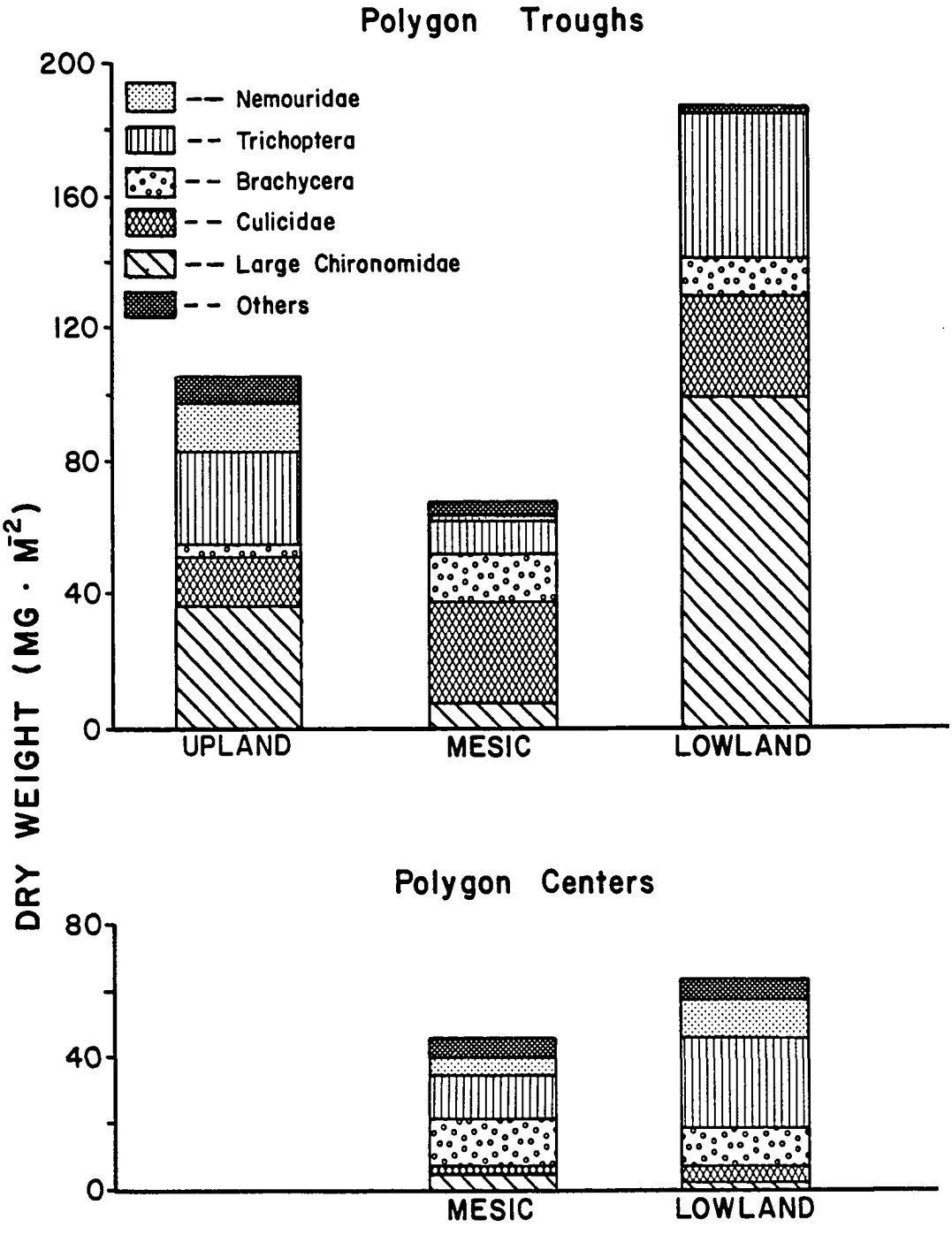


Figure 12. Aquatic insect emergence by plot and pond type, Canning River delta, 1980.

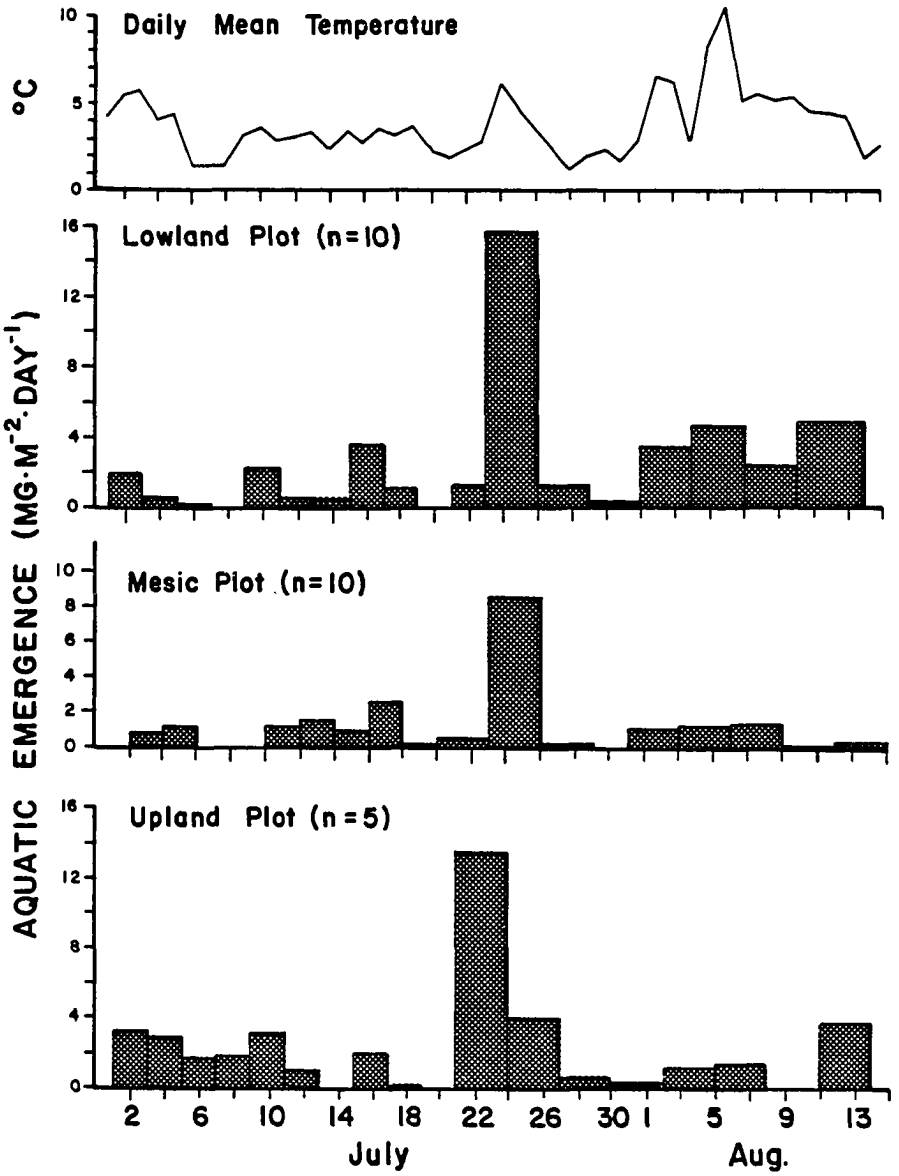


Figure 13. Timing of aquatic emergence by plot and pond type, Canning River delta, 1980, with daily mean temperature from 1 July to 15 August.

84% (mesic) of the total emerging chironomid biomass for the season. An even warmer spell in early August was accompanied by an increase in insect emergence only in the lowland where midges, mosquitos, and caddisflies were captured in large quantities.

Other Arthropods

At Barrow, the limnephilid caddisfly Lenarchus expansus emerges from saturated soil, rather than the truly aquatic habitats characteristic of its order (MacLean and Pitelka, 1971). Limnephilid caddisflies, possibly this species, were collected from terrestrial emergence traps in very wet sites at Canning River delta. All but two of the 31 specimens collected in terrestrial traps were from the lowland plot, where densities from traps in the wettest class were $11/m^2$. With a mean individual dry weight of approximately 2.0 mg, this represents a considerable contribution to total emerged insect biomass. I have included this taxon in the summary, Table 15.

Other terrestrial taxa used by birds include arachnids, carabid and staphylinid beetles, sawflies (Tenthredinidae), and a variety of dipterans such as Chironomidae and Muscidae (Holmes and Pitelka, 1968). In the aquatic systems, I sampled only the pond edges and there is evidence that the macrobenthic assemblage of invertebrates of pond centers is qualitatively different from that at the pond edge (Butler et al., 1980). Of the birds included in this study, only phalaropes are able to exploit the pond center fauna when water is high, but when pond sediments are exposed other birds are able to use this food resource. Adult midges emerging from pond centers could be a significant contribution

to the available surface prey, as well. Because the terrestrial taxa listed above were not sampled and pond centers were not sampled, my estimates of available surface prey are probably underestimates.

Summary

Table 15 shows the estimate for mean emerged insect biomass for the three study plots. These estimates are based on the proportion of habitat classes and biomass densities specific to these classes for each plot. Classification of habitat was by segment of the first DECORANA axis for terrestrial sites, modified by my on-site designation of "pond edge (polygon basin)" sites, which were placed in a class of their own for consistency with the insect sampling design. Trough edge occurred so rarely in my vegetation sample, which served as the basis for apportionment of habitat types, that I resorted to aerial photos (scale of 1:6,000) of the study plots to estimate their abundance. I used a dot grid with 440 points and counted number of sample points falling in trough habitat, for each plot.

Table 15 shows that the mean biomass of emerged insects ranges from 12 to 29 mg dry wt/m^2 on the three study plots. Terrestrial emergence exceeded aquatic emergence only on the upland plot despite the relatively small proportion of aquatic habitat. The lowland plot had the richest prey base for birds by virtue of both the greater area of aquatic habitat (Table 15) and the high level of production of adult insects from aquatic sites.

Table 15. Contribution of insect groups and microhabitat classes to total emerging insect biomass in the upland, mesic, and lowland plots. Total contribution to emerging biomass equals mg/m^2 per microhabitat class (from Tables 8,9,14) x proportional representation of microhabitat class.

	Terrestrial					Aquatic			Insect Group Total
	Dry----------				----------Wet	Basin	Trough	Pond	
	1	2	3	4	5	Edge		Center	
Upland Plot									
Proportional representation of microhabitats (%)	37	46	11	1	0	0	5	0	---
Total contribution to emerging biomass (mg/m^2)									
Pedicia	0.00	0.00	0.12	0.13	--	--	--	--	0.25
Tipula	4.57	1.44	0.00	0.15	--	--	--	--	6.16
Limnephilidae	0.00	0.00	0.00	0.00	--	--	--	--	0.00
Aquatic insects	--	--	--	--	--	0	5.3	?	5.30
Microhabitat Total	4.57	1.44	0.12	0.28	0	0	5.3	0	11.71
Mesic Plot									
Proportional representation of microhabitats (%)	3	43	28	8	3	5	7	3	---
Total contribution to emerging biomass (mg/m^2)									
Pedicia	--	0.12	0.00	0.37	0.15	--	--	--	0.64
Tipula	--	2.67	2.12	0.00	0.00	--	--	--	4.79
Limnephilidae	--	0.15	0.00	0.00	0.01	--	--	--	0.16
Aquatic insects	--	--	--	--	--	2.24	4.80	--	7.04
Microhabitat Total	0	2.94	2.12	0.37	0.16	2.24	4.80	?	12.63
Lowland Plot									
Proportional representation of microhabitats (%)	0	16	16	28	10	16	5	9	---
Total contribution to emerging biomass (mg/m^2)									
Pedicia	--	0.23	0.21	1.11	3.68	--	--	--	5.63
Tipula	--	0.00	0.00	0.00	0.00	--	--	--	0.00
Limnephilidae	--	0.00	0.74	1.31	2.67	--	--	--	4.72
Aquatic insects	--	0.00	--	--	--	10.13	9.35	?	19.48
Microhabitat Total	0.00	0.23	0.45	2.42	6.35	10.13	9.35	?	29.43

Birds

Nesting Density

Breeding densities for all birds found nesting on the three tundra census plots are presented in Table 16. The density figures are minimum estimates since I cannot be certain that all nests in the study plot were actually located. For this reason I have indicated species for which nests are likely to have been missed (for 1980 only). These judgments were made on the basis of behavior of birds seen consistently in a particular portion of the study plot. For all density calculations and further discussion I have used the conservative figure for known nests, as presented in Table 16.

The data presented in Table 16 show differences between the plots in species composition and density of breeding birds. In the lowland plot, species richness was lowest and Red Phalaropes were the most numerous breeder. Red Phalaropes nearly doubled their breeding density from 1979 to 1980. Lapland Longspurs, Pectoral Sandpipers, and Red-necked Phalaropes also nested in the lowland plot. Dunlins may have nested there, although a nest was never found, and they certainly used the area when they were attending broods.

The upland plot had intermediate species richness but lower overall nest density. Lapland Longspurs were the most numerous species and Semipalmated Sandpipers (which did not breed at all in the lowland) were the most numerous breeding shorebird. The presence of thermokarst pools in the upland provided some wet habitat which was used by both

Table 16. Number of nests found in census plots, Canning River Delta, 1979-1980. Densities expressed in nests per km^2. For 1980, a single asterisk (*) indicates that an additional nest was probably present in the plot but not located. These additional nests not included in density calculations.

	1979				1980					
	Upland		Lowland		Upland		Mesic		Lowland	
	# nests	(nests/km^2)	# nests	(nests/km^2)	# nests	(nests/km^2)	# nests	(nests/km^2)	# nests	(nests/km^2)
Oldsquaw	0		0		0		1	(3.9)	0	
King Eider	0		0		0		1	(3.7)		
Rock Ptarmigan	0		0		1	(3.9)	1*	(3.9)	0	
Lesser Golden-Plover	1	(3.9)	0		0		1	(3.9)	0	
Semipalmated Sandpiper	2	(7.8)	0		6	(23.5)	5*	(19.5)	0	
Pectoral Sandpiper	0		3	(11.1)	1	(3.7)	8	(31.2)	4	(14.8)
Dunlin	1	(3.9)	0		1	(3.7)	2*	(7.8)	0*	
Buff-breasted Sandpiper	1	(3.9)	0		0		2	(7.8)	0	
Red-necked Phalarope	1	(3.9)	3	(11.1)	0		2	(7.8)	1	(3.7)
Red Phalarope	2	(7.8)	7	(25.9)	2	(7.8)	0*		13	(48.1)
Lapland Longspur	5	(19.6)	3	(11.1)	9*	(35.1)	13*	(50.7)	6*	(22.2)
Total	13	(51.0)	16	(59.2)	20	(78.1)	35	(136.5)	25	(92.5)

phalaropes and Pectoral Sandpipers. There was considerable change in species composition from 1979 to 1980; Lesser Golden-Plovers, Buff-breasted Sandpipers and Red-necked Phalaropes bred on the upland plot in 1979 but not in 1980. The Pectoral Sandpiper bred there in 1980 but not in 1979.

The mesic plot, censused only in 1980, had the greatest species richness and the highest overall nesting density. All of the shorebirds nesting in the other two plots also nested in the mesic plot, with the possible exception of the Red Phalarope which was not a confirmed breeder in the mesic plot. Species characteristic of the upland plot (Lapland Longspur, Lesser Golden-Plover, Buff-breasted Sandpiper, Dunlin) nested on the mesic plot in equal or greater numbers. Species characteristic of the lowland (Pectoral Sandpiper, Red-necked Phalarope) also nested there in equal or greater numbers.

Use of Habitat by Breeding and Transient Birds

Results of tundra plot censuses are contained in the Appendix and summarized in Figure 14. Bird use (based on mean seasonal density) for the mesic and lowland study plots (both years) was of similar magnitude, approximately 200 birds/km^2 . On the upland plot, bird use was only 55-70% of this level.

Figure 14 shows seasonal changes in density of Lapland Longspurs and shorebirds (all species combined) on the study plots. Longspurs have been separated from shorebirds because the numerical dominance of the former would obscure population shifts of the latter. Since censuses were not begun until late June in 1979, data for early June is

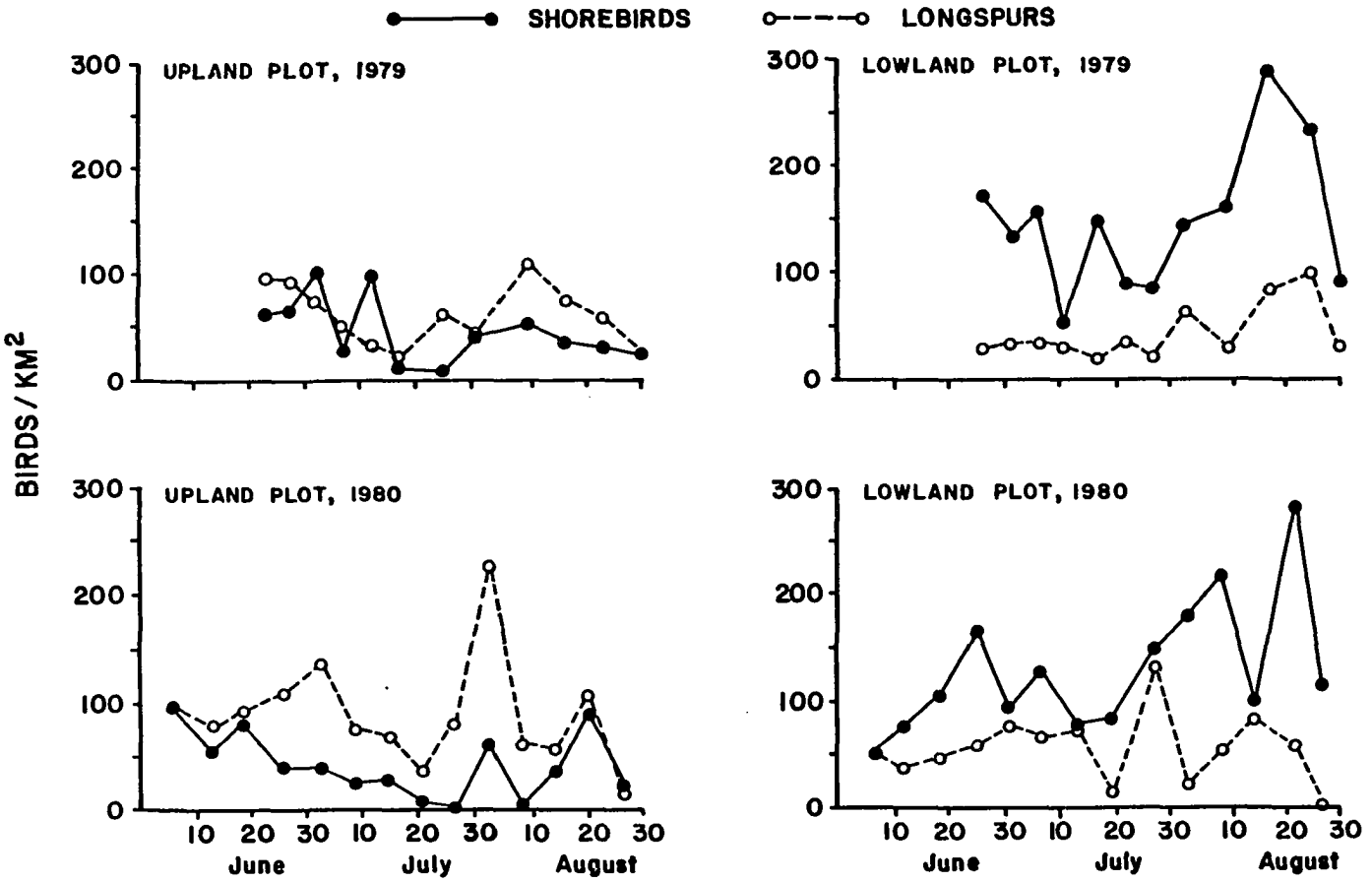


Figure 14. Seasonal trends in numbers of Lapland Longspurs and shorebirds on study plots at Canning River delta, 1979 and 1980. Continued on following page.

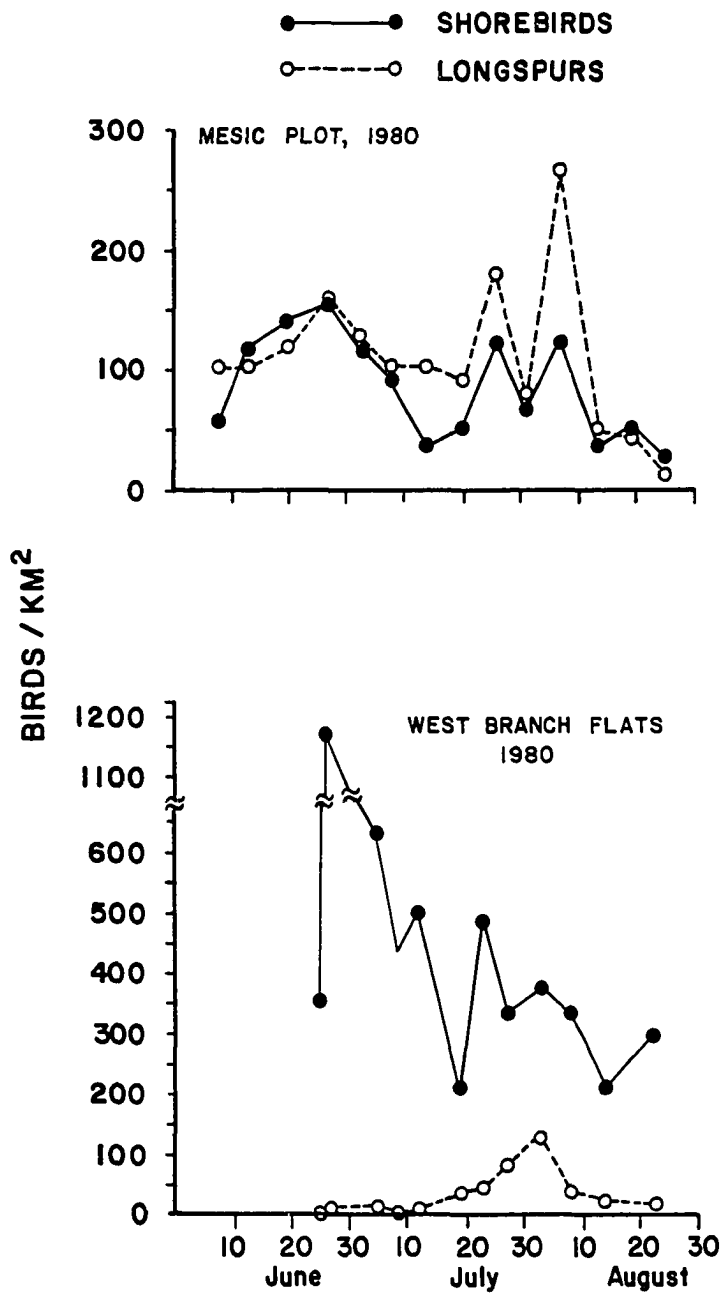


Figure 14. (cont.)

available only from 1980. In the early melt-off period in 1980, the upland plot received the greatest bird use, as indicated by the census on 6 June. After this initial census, shorebirds declined on the upland plot but increased rapidly on the mesic and the lowland plots through the month of June. Around 15 July, corresponding to the period of shorebird hatching and chick growth, shorebirds abandoned the upland plot and similar though less drastic declines in shorebird numbers occurred in the mesic and lowland plots. From late July through the end of August, the trend in bird use of the lowland diverged sharply from that of the upland and mesic plots. Shorebird numbers on the lowland plot were two to three times higher in late summer than June and July. This August shorebird peak was less apparent on the mesic and upland plots.

Longspur numbers in early summer were similar in the upland and mesic plots and lower in the lowland plot. High nesting density in the mesic plot was probably responsible for somewhat higher overall numbers of Lapland Longspurs recorded there through mid-summer. Lapland Longspur numbers peaked most strongly on the upland and mesic plots, although there was a substantial increase in Lapland Longspur use of the lowland plot in late summer, as well. In both the upland and lowland plots there was a more pronounced fall peak of Lapland Longspurs in 1980 than in 1979.

The results of the 1980 census on the West Branch flats are presented in the Appendix and Figure 14. The value for Semipalmated Sandpiper (and hence for total shorebirds) for 27 June is suspect; I

believe it to be an overestimate. In subsequent censuses a standard route was traversed at a relatively constant speed, and combined with a deliberate effort to avoid duplicate sightings, this minimized the likelihood of inflated estimates. Since this area was used by relatively mobile transient birds in high densities, the problem of duplicate sightings could not be eliminated. Nevertheless, I am confident that the census accurately reflects high shorebird use of the area during early summer. Bird use of this area was at least twice as high as the lowland and mesic study plots.

The West Branch flats area was unique in several aspects of bird use. Both density and diversity of shorebirds using the area were very high. Shorebird numbers in early summer were an order of magnitude above those on the other plots, even allowing for some uncertainty in the counts of Semipalmated Sandpipers. Most of the shorebird population in early summer consisted of large phalarope flocks which gathered on the ponds in the area in late June and July. Large numbers of migrating Semipalmated Sandpipers used the area from mid-June to mid-July. Shorebird numbers remained greater than or equal to those on the lowland throughout August. Densities of Lesser Golden-Plover, Baird's Sandpiper, Dunlin, White-rumped Sandpiper, Western Sandpiper, Stilt Sandpiper, and phalaropes were higher here than on any other plot. Longspur numbers were generally low except for a brief period in late July and early August.

Although this analysis indicates some important differences between areas, some of the underlying seasonal population shifts are obscured

by combining shorebird species. Figure 15 shows seasonal changes in numbers of the most important shorebird species in both years.

Lesser Golden-Plovers (Fig. 15) maintained low densities on all plots during the breeding season, although no nests were actually located on the lowland. Eastward migration began in mid-July when flocks of adults appeared, and the juveniles followed in August. In 1979 there were two peaks on the lowland plot, one around 20 July representing adults, and a much larger peak in August representing the movement of juveniles. In 1980 more adults were seen (the peaks prior to 10 August represent adults) and fewer juveniles. In both years, however, the lowland was heavily used by Lesser Golden-Plovers in late summer, though not in early summer. Flocks fed actively on the study plots; residence time was difficult to judge but often the visits were very brief, on the order of several minutes to several hours, with a high turnover rate during peak migration periods. Lesser Golden-Plovers were one of the few species that continued to occur on the upland plot during the late summer migration period.

Buff-breasted Sandpipers were common on the upland plot in 1979, and were usually associated with upland sites throughout the summer. In 1979 there was a peak in early July on the upland plot (Fig. 15) probably representing movement of adult males after the courtship period was over. A second peak in early August probably represented movement of adult females and/or juveniles. Buff-breasted Sandpipers nested on the mesic plot but were seen only twice on the lowland plot in the two years of study.

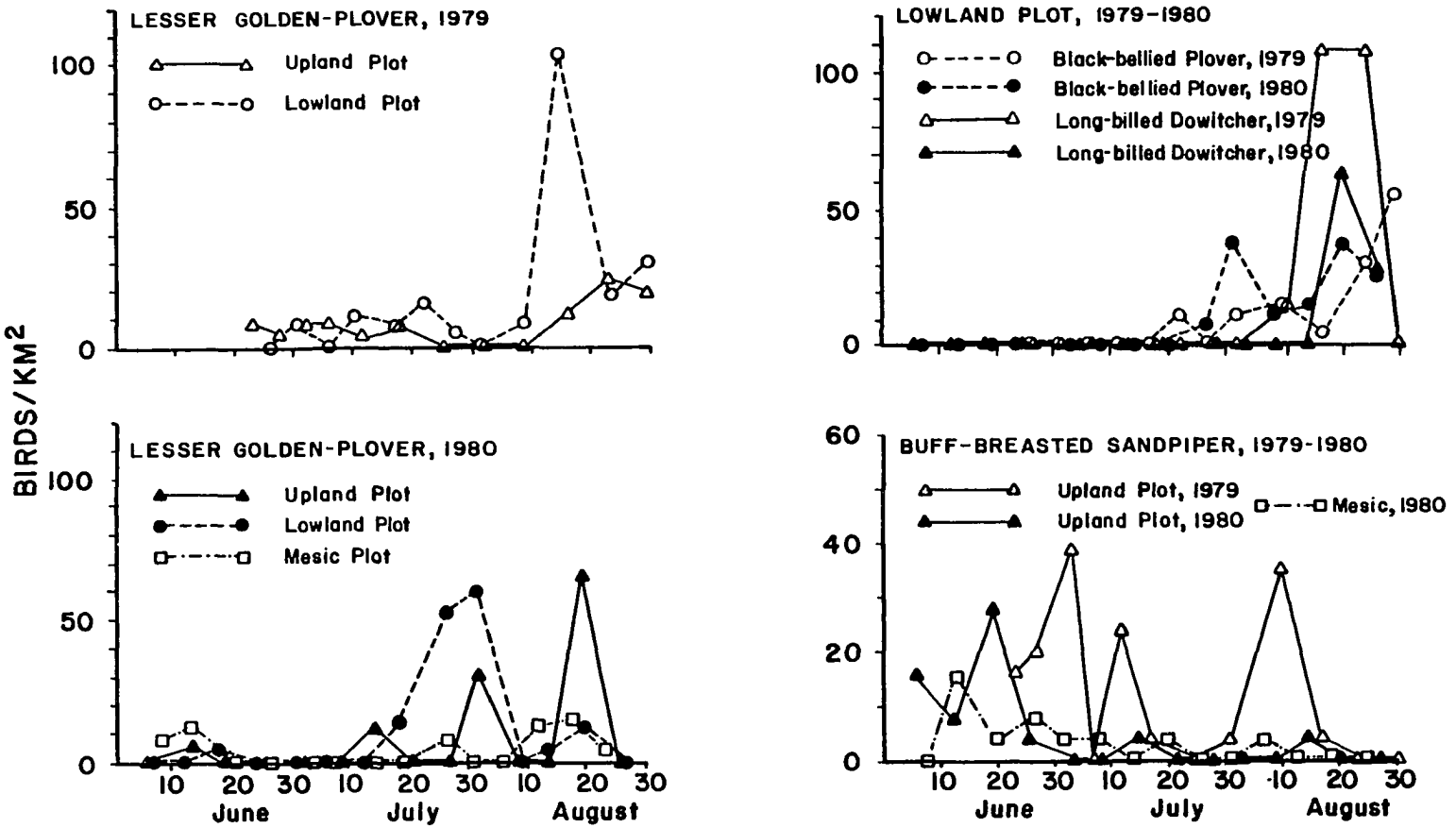


Figure 15. Seasonal trends in numbers of nine shorebird species, Canning River delta, 1979 and 1980. Note change of scale for Buff-breasted Sandpiper. Continued on following pages.

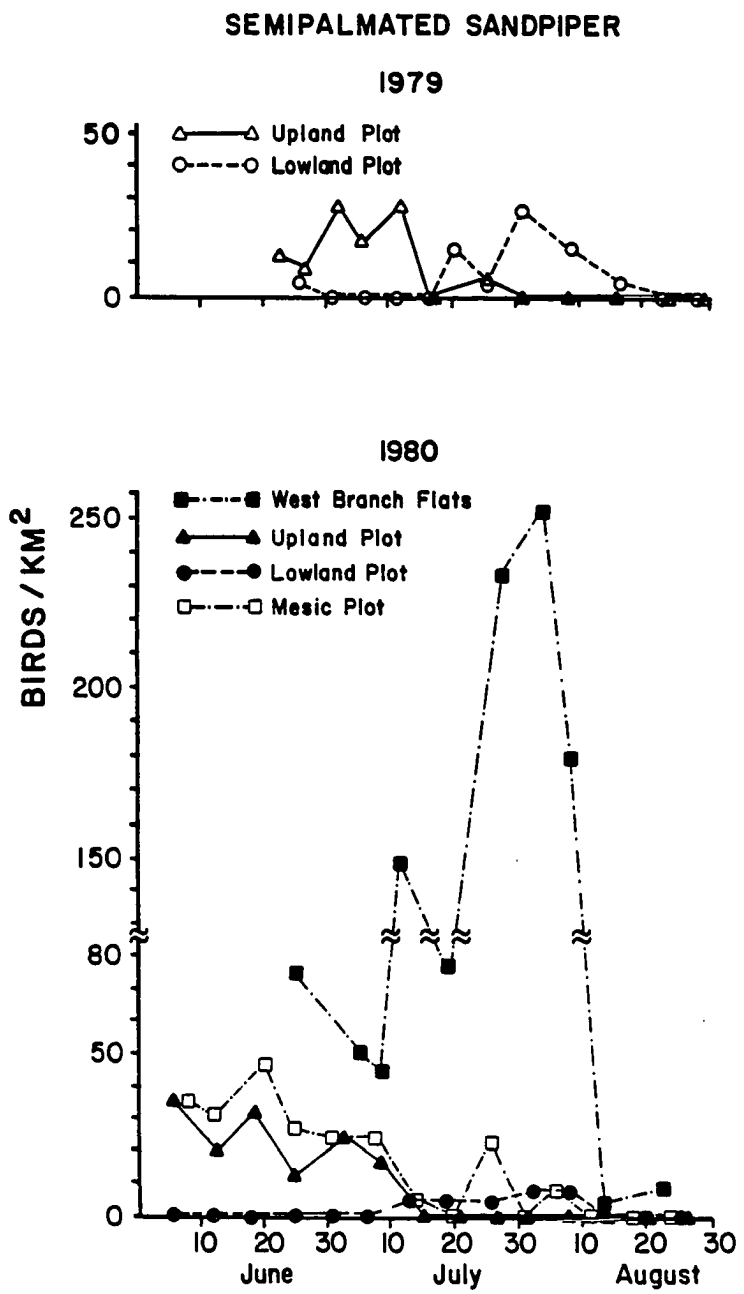


Figure 15. (cont.)

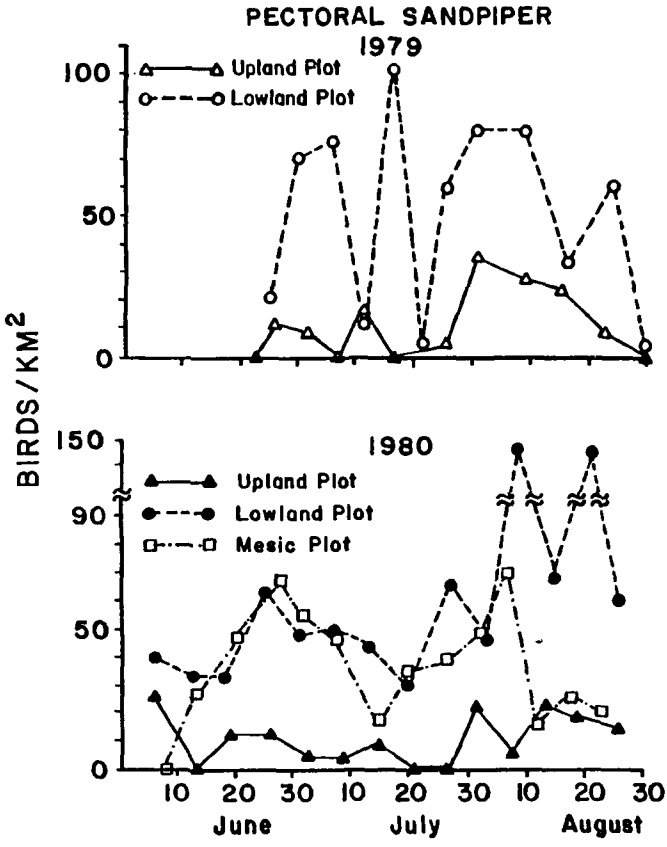
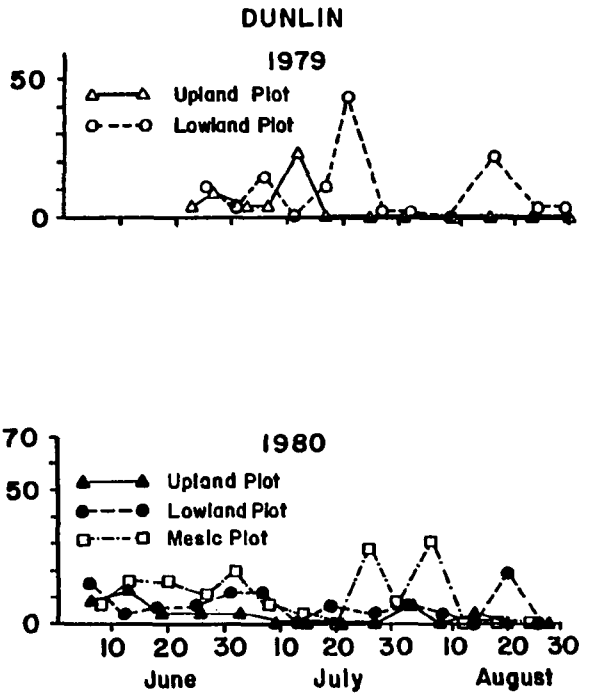


Figure 15. (cont.)


DUNLIN
1979
50
0
Upland Plot
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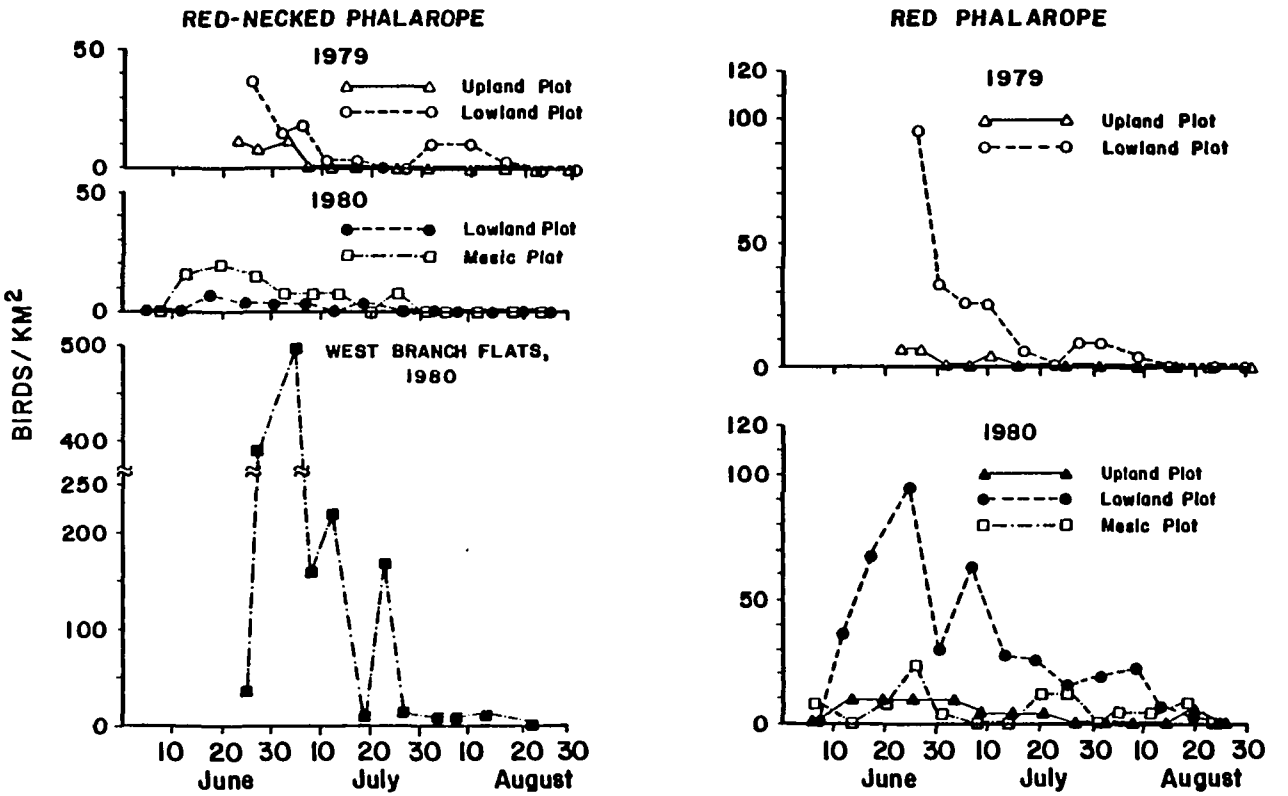

Figure 15. (cont.) Note change of scale for Red-necked Phalarope at West Branch Flats.

Semipalmated Sandpipers were present in fairly high numbers on the mesic and upland plots from early June to mid-July. After the young hatched in early June this species virtually disappeared from the upland plot. In both years the decline of this species on the upland plot was coincident with increased use of the lowland plot, although fewer were seen there in 1980 than in 1979 (Fig. 15). Semipalmated Sandpipers used the mesic plot later in the season than the upland plot; flocks of migrating adults were seen there in mid-July.

Dunlins (Fig. 15) were similar to Semipalmated Sandpiper in seasonal pattern of abundance except that they seemed to have broader habitat use patterns early in summer; they were found quite often in the lowland and may have nested there. Like the Semipalmated Sandpiper, they disappeared from the upland in mid-July. Both adults and juveniles used the mesic and lowland plots into mid-August. Both of these species made heavy use of marine littoral habitats in migration. Large numbers of Semipalmated Sandpipers used the West Branch flats area from mid-July to mid-August (Fig. 15), in concentrations far greater than those on the tundra study plots. Dunlins were less common in general, but fairly high concentrations were present on the flats in August.

Pectoral Sandpipers (Fig. 15) were most numerous overall on the lowland plot, although the mesic plot supported a higher nesting density. Transient Pectoral Sandpiper males moved through the area in late June to mid-July after which females, then juveniles, appeared in large numbers. In 1979 there was an intense period of migratory movement of adult females in mid-July with a longer period of movement of juveniles

in late July and August. In 1980 there was a less conspicuous movement of females but the peak of juvenile migration in August was very high, with densities exceeding that of any shorebird species on the tundra study plots. Although Pectoral Sandpipers used the upland plot very little in early summer (except during melt-off in 1980) the late summer influx of juveniles seemed to "spill over" into the upland. Although Pectoral Sandpiper numbers were relatively small in the upland plot, this species accounted for a substantial fraction of total shorebird use of that site. In contrast to Dunlins and Semipalmated Sandpipers, post-breeding Pectoral Sandpipers made very little use of the flats.

Red Phalaropes (Fig. 15) arrived later than other shorebirds and reached peak density on the tundra in late June. They were abundant only on the lowland plot but present in low numbers on the mesic plot. In both years one or two nests were located on the upland plot but transient phalaropes did not use the area. By early to mid-July the females left the tundra and there was a substantial decline in numbers on the plot. Males remained into August and fledged juveniles were commonly seen on the lowland plot during the first half of August.

Red-necked Phalaropes were less abundant than Red Phalaropes on tundra habitats at Canning River delta (Fig. 15). They were fairly common on the lowland plot in 1979, and seasonal changes in abundance parallelled those of Red Phalaropes. An unsuccessful nesting attempt was made on the upland in 1979, but otherwise this species did not use the area. Red-necked Phalaropes were less common in 1980 than in 1979; in 1980 they used the mesic plot most heavily. Both species, but Red-

necked Phalaropes in particular, used the flats extensively. Flocks composed primarily of females were present in late June and early July, and males and juveniles were found there from mid-July through mid-August.

Long-billed Dowitchers and Black-bellied Plovers (Fig. 15) occurred on the lowland plot during the late summer migration eastward. The flight of Black-bellied Plovers consisted mostly of adults, at least until about 20 August, and few juveniles were seen in 1980. Almost all of the Long-billed Dowitchers seen on the study plots were juveniles. The flight of Long-billed Dowitchers was earlier and more intense in 1979 than in 1980. These two species, along with Lesser Golden-Plover and Pectoral Sandpiper, represented the bulk of the late summer peak in shorebird use of the lowland.

ENERGETICS

Comparison of bird densities between habitats is one way of measuring the relative importance of habitats to birds. An approach oriented more towards ecosystem function is to compare bird biomass and estimate energy flow between trophic levels.

Energetics of four calidridine sandpipers was studied at Barrow by Norton (1973). He used gas exchange methods to measure metabolic rate in the Semipalmated Sandpiper, Baird's Sandpiper, Pectoral Sandpiper, and Dunlin. By dropping the temperature to which his experimental subjects were exposed, he determined maximal resting metabolic rates, which were considered to be equivalent to the maximal rate of long-term energy use. Because of the low ambient temperatures, long daylight hours of activity, and sequence of energy-demanding activities in which breeding birds are engaged, Norton argued that the free-living bird is probably performing at close to this maximum level throughout the breeding season. Independent calculations based on time-activity budget studies of Lapland Longspurs (Custer, 1974) and Semipalmated Sandpipers (Ashkenazie and Safriel, 1979a) yielded results very close to that obtained by Norton (for the sandpiper) and by extrapolation from his data (for the longspur).

I have adopted this assumption and used a regression model based on Norton's data to predict energy use by other shorebird species (and Lapland Longspur) occurring at the Canning River delta. When observed maximum resting metabolic rate (in terms of daily net energy require-

ments reported by Norton) is regressed on body weight (Fig. 16), the following relationship is obtained:

log Metabolic Rate = log 1.09 + 0.79 log Body Weight

I have used this simple equation as a model to predict energetic requirements of all birds recorded on the study plots. This model assumes a constant rate of energy expenditure, regardless of variation in activity budget or temperature. The slope of this regression line is slightly to considerably steeper than other models that have been developed (Lasiewski and Dawson, 1967; Kendeigh, 1970).

Values for body mass were obtained from the literature and are listed in Table 17, along with the net energy requirement predicted by the regression model. Net energy requirement was converted to gross energy requirement assuming a digestive efficiency of 0.75 (Alatalo, 1978).

The sum of the energy needs of all birds in a given environment may be termed the energetic demand of birds on that environment. For the purposes of this study, total energetic demand (ED) may be considered to derive from several components of the avian community:

ED(TOTAL) = ED(BREEDING ADULTS) + ED(MIGRANT ADULTS AND FLEDGED JUVENILES) + ED(CHICKS UP TO FLEDGING)

The level of the first two population components, in combination, were assessed through the periodic plot censuses. I assume each plot census represents the level of bird use for a period of days from the midpoint of the interval from the previous census to the midpoint of the interval to the following census. This period ranged from five to 10.5 days,

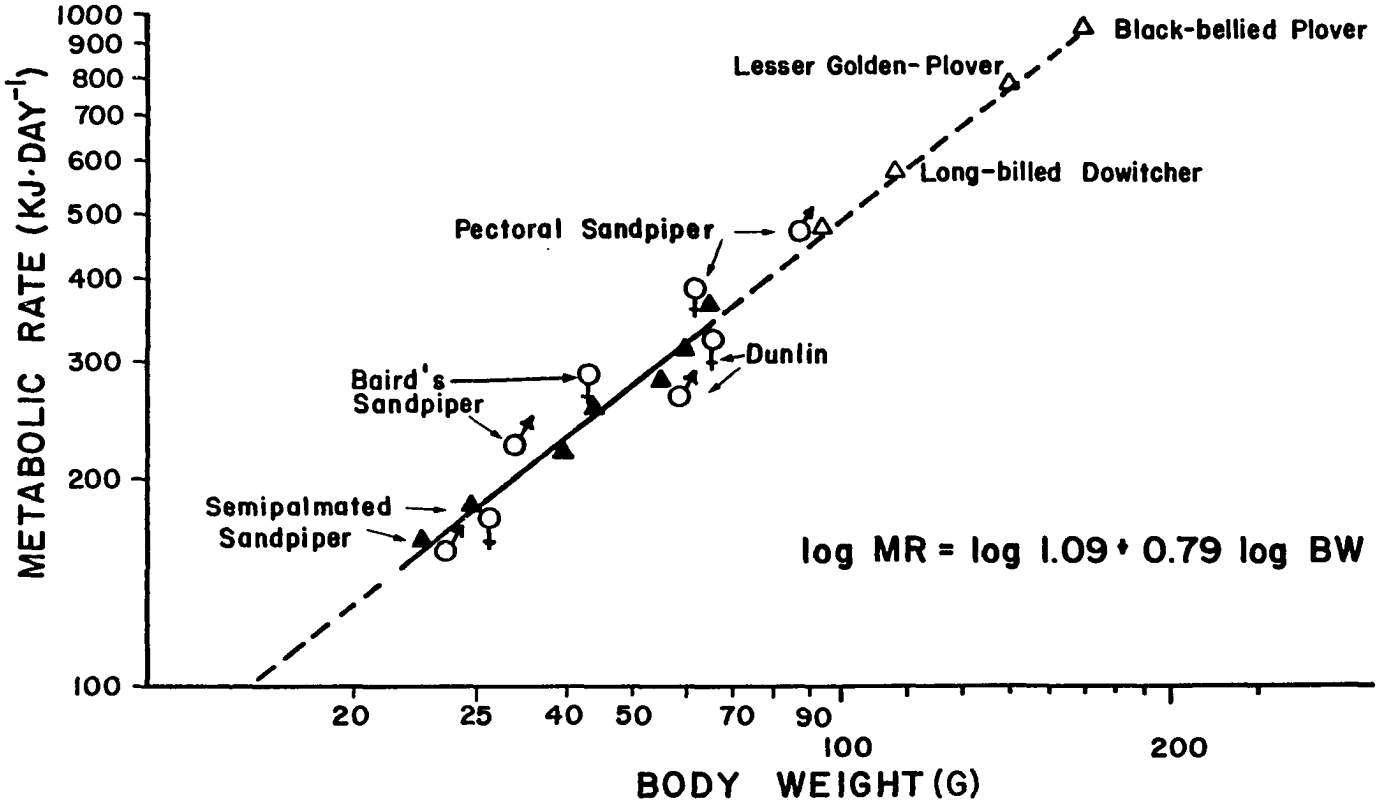

Figure 16. Regression of metabolic rate on body weight of shorebirds. Solid triangles represent data from Norton (1973); open triangles represent extrapolation based on weights listed in Table 17.

Table 17. Weights, energetic requirement, and breeding bird residence parameters used in energetic model. Weights are from Myers and Pitelka (1980) unless otherwise noted (mean of their weights for each summer month); weights in parentheses are means of appropriate age/sex class weights.

Species age/sex class	Body weight (g)	Gross energetic requirement (kJ/day)	Breeding Bird Residence			
			Arrival date	Residence Time (days) adult male	adult female	fledged juveniles
Black-bellied Plover						
ad.	236	1243	--	--	--	--
juv.	218	1166				
unid.	(222)	1205				
Lesser Golden-Plover			5 JN	50	50	10
ad.	166	941				
juv.	176	984				
unid.	(171)	962				
Whimbrel[1]						
ad.	400	1885	--	--	--	--
Semipalmated Sandpiper						
ad.	27	226	3 JN	50	32	10
juv.	24	200				
unid.	(26)	213				
White-rumped Sandpiper[3]			--	--	--	--
unid.	43	323				
Baird's Sandpiper			--	--	--	--
ad.	42	318				
juv.	33	218				
Pectoral Sandpiper			6 JN	25	60	15
ad. ♂	98	617				
ad. ♀	67	458				
unid. ad.	(82)	538				
juv.	71	480				
un. /juv.	(69)	469				
Dunlin			6 JN	70	70	30
ad.	58	410				
juv.	56	395				
un.	(57)	304				
Stilt Sandpiper[2]			--	--	--	--
ad. ♂	54	386				
ad. ♀	61	425				
un.	(58)	407				

Table 17. (cont.)

Species age/sex class	Body weight (g)	Gross energetic requirement (Kj/day)	Breeding Bird Residence			
			Arrival date	Residence Time (days) adult male	adult female	fledged juveniles
Buff-breasted Sandpiper			6 JN	30	65	10
ad.	58	420				
juv.	56	448				
unid.	(57)	434				
Long-billed Dowitcher			--	--	--	--
ad.	119	722				
juv.	102	640				
unid.	(110)	681				
Red Phalarope			8 JN	55	22	10
ad.♂	50	360				
ad.♀	61	429				
unid. ad.	(55)	358				
juv.	45	332				
unid. /juv.	(47)	346				
Red-necked Phalarope			8 JN	55	30	10
ad ♂	32	256				
ad.♀	36	280				
unid. ad.	(34)	268				
juv.	30	241				
unid. juv.	(31)	248				
Lapland Longspur[4]						
ad. ♂	28	230	1 JN	80	75	45
ad. ♀	25	210				
un. ad/juv.	(27)	224				

Sources:

1 (Johnson and Morton, 1976)
2 (Jehl, 1973)
3 (Palmer, 1967)
4 this study

with mode of five to six days. The census data yielded "bird-days" of use for each species, subdivided by age and sex class when possible. These values were multiplied by the appropriate daily energetic requirement (Table 17) and summed to yield estimates of the energetic demand of adult birds (breeders and migrants) and fledged juveniles, combined.

I estimated energetic demand of growing shorebird chicks by extrapolation from Norton's (1973) empirically derived data on Dunlin chicks. Table 18 shows the derivation of values for energetic demand of chicks up until reaching adult size, based on the ratio of weight gain of each species to that of Dunlin.

The population of pre-fledging chicks was largely unknown. Information on hatching success was of variable precision, and pre-fledging mortality completely unknown. I have assumed 50% pre-fledging mortality (approximating the value reported by Safriel (1975) for Semipalmated Sandpipers at Barrow), with deaths distributed randomly over the period of chick growth. This assumption results in a reduction of energetic demand of chick growth by a factor of 0.75 from the value that would be obtained from a model of 100% fledging success. Estimates of energetic demand of chicks span a range of values from the minimum, which counts only nests known to have had successful hatch, to the maximum, which counts all known successes plus all eggs in nests of unknown fate as "hatched."

Energetic demand of shorebirds and Lapland Longspurs on each study plot is presented in Table 19. Total energetic demand on the lowland plot is twice that on the upland plot, with the mesic plot falling in

Table 18. Weight data used to calculate gross energy of chick growth for shorebirds, extrapolating from Dunlin results in Norton (1973). Lapland Longspur data based on Custer (1974).

	Initial chick Weight (g)	Juvenile Weight (g)	Weight gain(g)	ratio to Dunlin	Gross Energy of chick growth (kJ/chick)
Lesser Golden-Plover	20[1]	176[2]	156.0	3.15	14,692
Semipalmated Sandpiper			21.7	0.44	2,063[3]
Pectoral Sandpiper			71.6	1.45	6,863[3]
Dunlin			49.5	1.00	4,750[3]
Buff-breasted Sandpiper	11[4]	65[2]	54.0	1.09	5,177
Red-necked Phalarope	4[5]	27	23.0	0.46	2,185
Red Phalarope	5[5]	45[2]	40.0	0.81	3,838
Lapland Longspur				N.A.	14,486

Sources:

1 Parmelee et. al., 1967
2 Myers and Pitelka, 1980
3 Norton, 1973
4 this study
5 D. Schamel, pers. comm.
6 MacLean, 1980 after Custer, 1974

Table 19. Estimated energetic demand (kJ/m^2) of avian insectivores by time period and for entire season. Range of values for chicks presented where necessary (see text).

	Upland		Mesic	Lowland	
	1979	1980	1980	1979	1980
Adults and fledged juveniles (by time period)					
1-15 June	--	0.78	0.82	--	0.64
16-30 July	--	0.63	1.31	--	1.12
1-15 July	0.62	0.43	0.85	0.96	0.99
16-31 July	0.29	0.41	1.05	0.91	1.49
1-15 August	0.77	0.66	1.01	1.74	1.60
16-31 August	0.55	0.79	0.35	2.74	1.94
Subtotal	--	3.70	5.39	--	7.78
Shorebird chicks	0.35-0.45	0.28	0.62-0.94	0.34-0.45	0.32-0.95
Longspur chicks	0.12	0.05	0.30	0.05	0.12
Total chicks	0.59	0.33	0.92-1.24	0.39-0.49	0.44-1.07
Total	--	4.03	6.31-6.63	--	8.22-8.85

between, despite higher breeding density. That the ranking of the study plots by breeding density differs from the ranking of plots on the basis of energetic demand suggests that it would be useful to separate the demand of transients from breeders. This cannot be done in a rigorous fashion because the distinction between breeder and migrant was not possible in the field. Individuals of species that did not breed in a plot may automatically be assigned to the "transient" category but a difficulty arises in categorizing individuals of species for which there was a local breeding population on the plot but transients were also present at times. To estimate the portion of ED(TOTAL) attributable to breeders I assumed values for residence time of breeding adults and fledged juveniles based on my field notes. These parameters are included in Table 17. The intent in my choice of values for these parameters was to obtain a reasonable but generous estimate of the energetic demand that could be ascribed to breeding birds. Calculations were based on the observed breeding density, assumption of maximum possible hatching success on the basis of available data, and fledging success assumptions identical to those above. These population parameters were combined with the residence times listed in Table 17 to yield energetic demand of the breeding birds of each species on each plot. When estimated energetic demand of breeders based on the above assumptions exceeded the estimate of ED(TOTAL) derived from the plot censuses for a particular species, the latter value was used. In practice, this restriction was invoked in most cases: i.e. all use of the study plot by species actually breeding within its boundaries could be

attributed to breeding adults and their young. Exceptions to this generality were Pectoral Sandpipers in all three plots and Lesser Golden-Plovers in the mesic plot, and some of the energetic demand attributed to transients is from these sources. Most of the energetic demand attributed to transients on each study plot derives from species which did not actually breed within the boundaries of the respective study plot. Thus, the very large share of total energetic demand attributed to transients is a result of heavy use by only a few species: Pectoral Sandpiper, Long-billed Dowitcher, Lesser Golden-Plover, and Black-bellied Plover. These species are important in terms of community energetics because of their abundance during migration and large individual size.

The share of the energy budget going to different sectors of the bird population is compared in Figure 17 for all three bird study plots in 1980. The relative proportion of energetic demand allocated to transients, as opposed to breeding birds (including young) was greatest on the lowland and least on the mesic plot. On the lowland plot, the energy removed from the system by transients exceeded that removed by breeding birds.

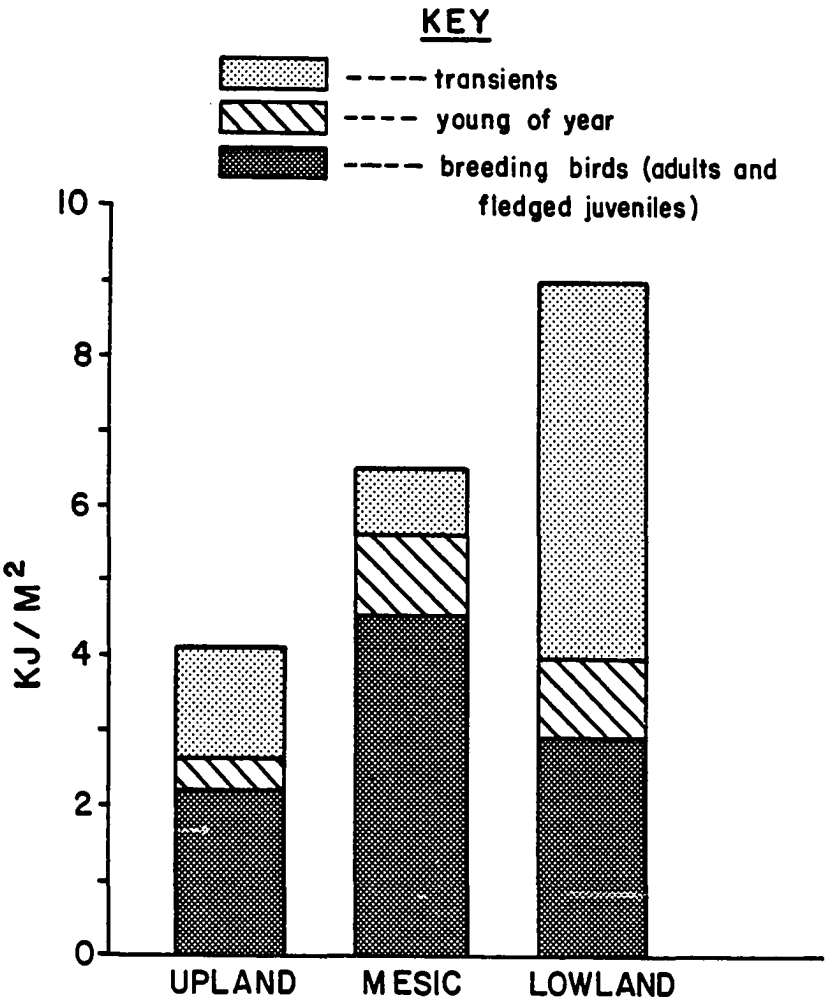

Figure 17. Sources of seasonal energetic demand by components of the bird populations using Canning River delta study plots, 1980.

DISCUSSION

I did not attempt to replicate bird censuses within habitats in this study; broad conclusions about habitat use based on results of a single census in each identified habitat type must necessarily be tentative. Some confidence in generalizing these conclusions may be gained to the extent that the results of this study are corroborated by other studies of birds on the arctic coastal plain. A summary of patterns of bird use observed at Canning River delta is presented below.

There is much variation in habitat use, both among plots and within plots over the course of the season. Viewing the study plots as representing a moisture gradient, the breeding birds can be roughly categorized in terms of their typical breeding habitat. "Upland" breeders are Lapland Longspur, Lesser Golden-Plover, Buff-breasted Sandpiper, Semipalmated Sandpiper, and Dunlin. "Lowland" breeders are Pectoral Sandpiper, Red-necked Phalarope, and Red Phalarope. All of these species, with the exception of the Red Phalarope, bred in equal or greater densities in the mesic plot than in either of the two plots with more extreme moisture conditions.

The Lapland Longspur, Lesser Golden-Plover, and Buff-breasted Sandpiper are prominent among upland breeders that may continue to use upland habitat in the post-breeding season. Dunlins and Semipalmated Sandpipers, on the other hand, shifted to wetter areas after the young hatched. Semipalmated Sandpipers shifted primarily to the marine littoral zone, while Dunlins were found more often on the tundra in late

summer. Holmes (1966a) reported that adult Dunlins remained on the tundra, while juveniles moved to littoral habitats, and this may have occurred at Canning River delta, as well.

The lowland breeders share the characteristic of parental care by adults of one sex only (Pitelka et al., 1974; Schamel and Tracy, 1977). Adult phalaropes of both sexes were present until late June, after which females gathered in flocks on large lakes and in marine littoral habitats. Male Pectoral Sandpipers left the breeding grounds in early to mid-July. This emigration by adult shorebirds resulted in a decline in bird use of lowland areas in mid-July, but other groups of birds moving into these habitats in mid- to late July offset the decline. These included adult female Pectoral Sandpipers (perhaps failed breeders or non-breeders), Semipalmated Sandpipers, and Lesser Golden-Plovers. In August, migrating flocks of adult and juvenile Black-bellied Plovers, Lesser Golden-Plovers, female and juvenile Pectoral Sandpipers, and juvenile Long-billed Dowitchers concentrated in wet areas. Lesser Golden-Plovers are enigmatic in that they may be found both in wet and dry sites in late summer. Myers and Pitelka (1980) noted great year to year variability in the extent to which Lesser Golden-Plovers used wet polygonized areas in August. Juvenile Long-billed Dowitchers typically fed in very wet areas; the intensity of the Long-billed Dowitcher influx can be grasped by noting that this species had the second highest seasonal mean density of any shorebird species on the lowland plot in 1979, although recorded on only three census dates. The combined populations of these species resulted in a sharp peak in use of the lowland area in late summer.

In general, this summary corresponds well to patterns of shorebird habitat use observed at Barrow (Myers and Pitelka, 1980), although there are differences in the abundance of certain species in the two areas. Red Phalaropes and Dunlins are more abundant at Barrow, and Red-necked Phalaropes are more abundant at the Canning River delta.

Both the upland and mesic plots contained a large proportion of dry or moist habitat relative to the lowland plot. Both areas had relatively high diversity of breeding bird species, and neither area attracted much post-breeding use by shorebirds. They differed in the greater use of the upland plot in early June, when more bare ground was available there, and in higher breeding density on the mesic plot. Physically, the mesic plot differed from the upland plot in having greater mean microrelief, more even distribution of microhabitats, more wet area, and less frost scar influence.

Can the differences in breeding density between these two plots be a result of these physical differences? Theory would predict greater species diversity in the more diverse habitat of the mesic plot, but the relationship of habitat diversity to density is not obvious. There is some support in the literature for the hypothesis that heterogeneity of microhabitat is correlated with higher breeding bird density on arctic coastal plain sites, as suggested by comparison of the upland and mesic plots. Myers and Pitelka (1980) used factor analysis to analyze habitat selection by shorebirds at Barrow and Atkasook on the arctic coastal plain. They found that the first two axes of ordination explaining most of the variability in shorebird use of habitat were "polygonization" and

"pondiness." The first axis represented a gradient from flat and poorly drained areas to areas which exhibited strong polygonization. The second axis represented a gradient from dry areas to those with a high proportion of the surface covered with ponds. At Barrow, they found relatively even distribution of shorebirds over "habitat space" during the nesting season; however, peaks were present in two portions of habitat space. One was in areas with a high degree of polygonization (i.e. microrelief features similar to those of the mesic plot) and the other peak was in areas of low to moderate relief polygons with many ponds (habitat similar to that found in the lowland plot). Spindler's (1978;1982) work at the Okpilak River delta, approximately 75 km east of the Canning River delta, offers some support for the hypothesis that microhabitat diversity is correlated with high breeding bird density; his "mosaic plot", which had high microhabitat diversity, also had higher nesting density (averaged over two years of study) of both shorebirds and Lapland Longspurs than two other census areas on the thaw lake plain.

The comparison between the mesic and lowland plots is more equivocal in terms of habitat heterogeneity. Although microrelief of the mesic plot exceeded that of the lowland, diversity (or more precisely, equitability) of microhabitat (Table 7) was higher on the lowland plot. The mesic plot was comprised mainly of moist to dry units, while the lowland was predominantly wet. In mid-June, about 70% of the lowland was flooded, greatly restricting foraging area for birds. The mesic plot had greater breeding species richness, suggesting that

fewer species can exploit the very wet habitat. Spindler (1978;1980) obtained a similar result; the only species consistently breeding in the wet areas were the two phalaropes and Pectoral Sandpipers. Interestingly, the Red Phalarope and Pectoral Sandpiper are two species that have exhibited the greatest year to year fluctuation in breeding density on study plots at Barrow (Holmes, 1966a; Pitelka et al., 1974; Myers and Pitelka, 1980) and both Red and Red-necked Phalarope breeding densities varied considerably on Seward Peninsula study plots (D. Schamel, pers. comm.). At the Okpilak study area, the "flooded plot" had the highest shorebird nesting density among three plots on the thaw lake plain in 1978, but the lowest in 1982. This decline was due to an 86% drop in Red Phalarope breeding density and 56% drop in Red-necked Phalarope density, only partially offset by an increase in Pectoral Sandpiper density (Spindler, 1982). At Canning River delta, Red Phalaropes doubled their nesting density on the lowland plot from 1979 to 1980. The picture that emerges is that lowland areas are capable of supporting high densities of breeding birds, but of only a few species. For unknown reasons, population levels of these species fluctuate dramatically. Thus, wet areas have the greatest variance in breeding bird density, with densities occasionally reaching very high levels.

While the hypothesis that microhabitat diversity is positively correlated with breeding density on the arctic coastal plain must be considered tentative, there is very strong empirical evidence for the generality of the late summer influx of transients in wet tundra areas along the Beaufort Sea coast. Myers and Pitelka (1980, p. 71) attempted

to define the geographical limits of this "corridor" of heavy post-breeding shorebird concentrations:

> Reports from other studies (Connors and Risebrough, 1976, 1977; S. G. Jones, pers. comm.) as well as our own observations away from the Barrow-Atkasook area indicate that the corridor extends laterally along the coast at least as far east as Prudhoe Bay and as far west as Icy cape, for a total of some 550 km...Work in the Prudhoe Bay area indicates a decrease in numbers only 25 km south from the coast and virtually no build-up only 50 km south (S. G.. Jones, pers. comm.).

A similar pattern was observed at the Okpilak River delta (Spindler, 1982), and it is evident that the corridor extends east at least to Barter Island. Results reported from Prudhoe Bay in 1981 (Troy and Johnson, 1982) do not conform to this pattern, except for increased numbers of Long-billed Dowitchers in August. The Prudhoe Bay results notwithstanding, the consistent reports from a number of locations suggest that the late summer concentration of shorebirds (and to some extent, Lapland Longspurs) is a real and general phenomenon along the Beaufort Sea coast of Alaska. Studies on the arctic coastal plain that restrict their consideration of bird distribution to breeding birds alone may emerge with a distorted picture of the importance of particular habitats to birds.

The results of bird census at the Canning River delta, at least partially substantiated by the results of other studies, suggest that high breeding populations of birds are associated with diversity of microhabitat and that there is extremely intense use of wet tundra areas by late summer transients. Thus, the areas most heavily used by tran-

sients are not necessarily the most attractive to breeding birds. Are there environmental factors that could plausibly account for these results?

Variability in food availability has been cited to account for differences in density of tundra nesting Dunlins (Holmes, 1970) and for seasonal shifts in habitat preference in shorebirds at Barrow (Holmes and Pitelka, 1968). Seastedt and MacLean (1979) demonstrated an inverse relationship between average food availability and territory size in Lapland Longspurs at Barrow, which implies a positive relationship between food availability and breeding density, provided the habitat is saturated with longspurs. Insect emergence was sampled at the Canning River delta as an index of food resources in various microhabitat types and in the study plots as a whole. This discussion will focus on crane flies and midges, since collectively they are the most important prey types.

As an aid to interpretation of the 1980 emergence of crane flies at Canning River delta, it is useful to compare the results with those from other sites. Density of emerging Tipula ranged from 0-18 individuals/m^2 and averaged about 3.0 individuals/m^2 at Barrow (MacLean, 1980) and a similar average was found at Prudhoe Bay (MacLean and Ayres, 1982). Density of emerging Pedicia was 0-30 individuals/m^2 in a variety of habitats at Barrow and averaged 11.5 individuals/m^2 . At Prudhoe Bay, numbers averaged 2.8 individuals/m^2 (MacLean and Ayres, 1982). Crane fly emergence at Canning River delta in 1980 presents a contrast to emergence patterns reported for Barrow and Prudhoe Bay. The median date

of emergence for Pedicia was 3-4 July, seven to twelve days earlier than reported from Barrow or Prudhoe Bay, except for Prudhoe Bay in 1971 when median emergence was also very early (MacLean, 1975). The median date for Tipula was 10 July, a more "normal" result, but the sample size was miniscule (12 individuals). Density of Tipula ranged from 0-1 individual/m^2 and the mean was 0.37 individuals/m^2 . Density of Pedicia ranged from 0-9 individuals/m^2 with a mean of 1.76 individuals/m^2 . Both the early median date of emergence and the low densities relative to the other study sites suggest that total emergence at Canning River delta was reduced by the onset of cold weather around 4 July, 1980.

The high degree of synchrony typical of crane fly emergence has led MacLean (pers. comm.) to postulate that timing of emergence is controlled in a two-step fashion. First, there is a minimum accumulated metabolic heat sum needed in order to complete pupation up to the point of ecdysis from the pupa. However, actual timing of emergence is triggered only after the pupa is exposed to some threshold temperature. This temperature must be high enough to actually synchronize the adult population and to assure emergence into warm enough conditions to allow completion of the life cycle; it must be low enough to do this consistently, even in relatively cool seasons. A similar mechanism has been proposed for emerging chironomids (Danks and Oliver, 1972).

Aquatic emergence at Canning River delta was depressed during the period 4-22 July but a pulse of emergence was evident 23 July, when temperatures warmed (Figure 10). In contrast, crane fly emergence accelerated in the period 2-3 July, but then tapered off and fell to prac-

tically none by 15 July, and did not recover. This suggests that the larvae had entered the pupal stage, but with the exception of the individuals that completed pupation earliest, failed to reach the threshold temperature for emergence within some critical period. That the pulse in aquatic emergence on 23 July was not accompanied by a pulse in crane fly emergence suggests that there was widespread pupal mortality. Unfortunately, this interpretation of emergence results was not tested by sampling the soil for pupae in late summer.

An alternative interpretation is that Tipula, in particular, is not as abundant at Canning River delta as at Barrow and Prudhoe Bay. Certainly, Tipula is not universally abundant in all tundra areas; Holmes (1970) found that sod-dwelling larvae were virtually absent from his study area in the Yukon-Kuskokwim delta region. Furthermore, the abundant member of this genus at Barrow, Tipula carinifrons, is largely replaced by Tipula arctica at Prudhoe Bay (MacLean and Ayres, 1982). The large wetland-inhabiting crane fly, Prionocera, is reasonably abundant at Barrow but was hardly found at all at Prudhoe Bay (MacLean and Ayres, 1981) and never trapped at Canning River delta. It is clear that the composition of the crane fly fauna of the arctic coastal plain should not be assumed uniform. More intensive sampling for several years would be needed to fully address the question of comparative abundance of Tipula, but it seems extremely unlikely that densities should be so similar at Barrow and Prudhoe Bay, yet an order of magnitude lower at Canning River delta. Casual observation at the Canning River delta in 1979 suggested that more adult crane flies were present in that year.

The likelihood of cold weather reducing crane fly emergence to the levels observed at Canning River delta can be evaluated by examining the year to year variability in emergence at Barrow. Table 20 shows the biomass of Tipula and Pedicia captured at Barrow in 1969 (an exceptionally cold year) versus mean biomass captured during 1967-1968, 1970-1971, and 1975 (Seastedt and MacLean, 1979). In 1969, Tipula emergence was reduced to 20-25% of the average. Pedicia numbers were also reduced, but not to such an extent. A reduction of Prudhoe Bay and Barrow Tipula densities by a factor of five would yield a value in the same order of magnitude as emergence at Canning River delta. Based on the variability of emergence at Barrow, it seems likely that crane fly emergence at Canning River delta was depressed by cold weather to abnormally low levels.

The impact of cold weather on the availability of prey would be most severe during early to mid-July, when both Lapland Longspurs and shorebirds are dependent on surface-active insects. The results of the Canning River delta study indicate that food supply could indeed be inadequate at this time. Converting average prey biomass density (from Table 15) to energetic equivalent at a conversion rate of 23 kJ (5.5 kcal) per gram (Custer, 1974), average available energy was 0.27, 0.29, and 0.68 kJ/m^2 on the upland, mesic, and lowland plots, respectively. These values are below the calculated energetic demand of chicks alone (Table 19) on the upland and mesic plots and within the range of demand values for chicks on the lowland plot. This implies that food availability on at least two of the Canning River delta study plots was

Table 20. Biomass (mg) of Tipula and Pedicia captured on sticky boards in wet, mesic, and dry habitats in Barrow, 1969 vs. 1967-1968 and 1971, 1972, and 1975.

	Tipula		Pedicia	
	1969	other years	1969	other years
Wet	229	1063	191	310
Mesic	318	1758	83	211
Dry	534	2023	27	71

insufficient to support 50% fledging success. This comparison is conservative in that it ignores predation on surface active insects by adults and assumes a generous digestive efficiency of 0.75, which may overestimate the digestibility of adult insects with much of their mass in relatively undigestible skeletal structures. A further refinement may be in order -- Seastedt and MacLean (1979) showed that nestling Lapland Longspurs were fed largely on crane fly pupae, a resource which, if anything, should have been available in greater than usual abundance if the scenario of cold-induced failure of emergence is correct. Subtracting the energetic demand of Lapland Longspur chicks changes the magnitude of food supply relative to the needs of chicks, but the supply and demand values are close enough in all cases to suggest possible food limitation. Typically, the tundra in July may be aswarm with insects, but under conditions similar to those of 1980 at Canning River delta, food for birds may be scarce enough to limit reproductive success.

An unexpected result of the insect sampling was that in spite of the small areal extent (5.0 - 21.0 %) of pond edge habitat, 45-60% of the emerged insect biomass was produced in aquatic habitat. Chironomid production at three Barrow ponds was estimated at 1.0-2.0 g dry wt./m^2 of emerging adults (Butler et al., 1980). This is two orders of magnitude greater than the biomass of emerged crane flies at Barrow and Prudhoe Bay. This suggests that in a poor year for crane fly emergence, aquatic insects may be an essential food for newly hatched birds. This would be particularly true if poor years for terrestrial emergence were not necessarily poor years for aquatic emergence. The results of this

study show that the two are not necessarily temporally coupled within a season, but there are no available data on how closely aquatic emergence tracks terrestrial emergence from year to year.

For a breeding shorebird, there are somewhat conflicting habitat requirements to be satisfied. During early summer, drier habitats are important because they are snow-free and dry sooner than lowlands, and they are the best source of large Tipula larvae and pupae. Adult insects are not yet available, and midge larvae are largely inaccessible due to high water. However, for brood rearing, access to troughs and ponds may be important, both as a supply of food for the young and for the protection from predators afforded by the lush vegetation. Norton (1973) and MacLean (1980) have emphasized the foraging efficiencies accrued by a bird feeding on the large packets of energy embodied in crane flies, as opposed to the smaller insects. An area with moist and dry microsites produces high emerged insect biomass in a year of at least average Tipula emergence, because of the large individual size of these insects. As a result, in many years mesic sites should be attractive brood-rearing habitat. However, in a poor year, or at any time when cold weather restricts the availability of adult crane flies, aquatic emergents are essential prey items. The best "bet-hedging" choice for a bird would be to nest in an area which included both wet and dry sites, and this could be a factor leading to high nesting densities in highly polygonized areas. This study suggests that thermokarst pools in polygon troughs may be a particularly productive habitat for prey species. If this proves to be the general case, then habitats such as

high relief polygons with thermokarst pools should be exceptionally attractive breeding habitat, incorporating the best of both crane fly and midge habitat.

Feeding ecology studies at Barrow have shown that calidridine shorebirds feed on midge larvae, if accessible, from mid-July through the end of summer (Holmes and Pitelka, 1966). The use of very wet tundra by shorebirds at Canning River delta in late summer suggested that they, also, are probably feeding mainly on midges. Availability of midge larvae depends primarily on water levels of ponds; if low, then pond sediments are exposed, making midges available to foraging birds. If water levels are high, this may prevent birds from foraging on midges. In this regard, the configuration of pond margins affects the availability of midges. Compared with gently contoured shorelines of ponds in polygon basins, steep-banked ponds such as thermokarst pools provide less area for foraging because less area of pond sediment is exposed per unit drop in water level. This points out a seasonal difference in the value of thermokarst pools and troughs as foraging habitat; they are especially productive in mid-July, when adult insects disperse onto adjacent tundra, but they provide a poorer habitat for foraging on larval insects in late summer. The mesic and lowland plots presented a contrast in this regard. Not only did the mesic plot have less pond area, but the ponds tended to be steep-banked in the mesic plot, providing less littoral habitat than ponds in the lowland plot. This is consistent with the observation that the mesic plot had high breeding bird density but little post-breeding use, while the lowland

plot received very heavy use in late summer.

The food resources represented by midges of pond sediments, when available, are enormous. Butler (1982b) studied two sibling species of the genus Chironomus, large midges that inhabit the sediments of pond centers. These species have seven-year life cycles, with three years spent in the fourth and final instar. Late summer individual dry weights of the oldest cohort of larvae averaged 3.44 to 5.48 mg in three different years. Biomass of the final instar (three age-classes) was on the order of 7,000 mg/m^2 . These larvae are approximately equal in size to the crane fly Pedicia hannai but are present in numbers much greater than Pedicia even at peak abundance of the latter. Biomass of these midges was 20 times that of Pedicia, and 14 times that of Tipula carinifrons at Barrow (Butler, 1982b; MacLean,1980). When water levels are such that midge larvae are available, the inefficiency of foraging for small prey (relative to Tipula) is far outweighed by the advantage of greater prey density. Migrants are not subject to the travel costs constraining nesting birds, which must return to a central place, and should be free to capitalize on newly exposed sediments in mid-summer when water levels often recede in ponds (Figure 6). The magnitude of food resources available in pond sediments far exceeds that of terrestrial habitats. Thus, we should expect heavily ponded lowland areas to attract birds in late summer when water levels fall sufficiently to allow exploitation of this resource.

Butler (1982a) found several species of midges with prolonged life cycles at Barrow and Prudhoe Bay, notably the sibling species of the

genus Chironomus, mentioned above, with a seven year life cycle. These appear to be geographically restricted, as described by Butler (1982a, p. 68):

> The coastal tundra of northern Alaska has an extreme climate, even relative to regions only a few dozen kilometers inland, but no populations of these Chironomus species have been found in ponds farther than about 20 km from the coast, despite of a search as far as 220 km south of Prudhoe Bay during 1979. In general, species shifts as well as life history changes appear to be associated with the transition from ponds in the wet coastal zone to those of the moist inland tundra. It seems plausible that these species of Chironomus may be geographically restricted to the narrow band of coastal tundra and that such a long life cycle may be a normal aspect of their population biology throughout this range.

The co-occurrence of midge species with multi-year life cycles in a narrow band along the Beaufort Sea coast would result in high and stable food biomass in this area for birds. The geographic coincidence of the range of these midges and the area heavily used by post-breeding shorebirds is highly suggestive. The Beaufort Sea coast may be an important area for birds precisely because of the "unfavorable" environmental conditions which cause slow growth rate and short growing season for their prey.

SUMMARY AND CONCLUSIONS

The purpose of this study was to compare bird use of arctic tundra habitats. This was accomplished by censusing plots with differing habitat characteristics with respect to wetness and microtopography. An upland and a lowland site were censused in both 1979 and 1980 and a mesic site was censused in 1980 alone. In both years, the upland site had greater diversity of breeding species but lower breeding density. Species with upland affinities were Lesser Golden-Plover, Semipalmated Sandpiper, Buff-breasted Sandpiper, and Lapland Longspur. Species with lowland affinities were Pectoral Sandpiper, Red-necked Phalarope, and Red Phalarope. All of these species bred in the mesic plot in densities equal to or greater than those in the other plots.

Use of the plots by both breeding birds and transients, combined, was greatest on the lowland plot. The upland plot attracted more birds only in early June when other areas were snow-covered or flooded. Greater use of the lowland from mid-July to late August resulted from upland breeders shifting to wetter habitats during and after brood-rearing and massive influx of transients, mostly Lesser Golden-Plovers, Black-bellied Plovers, Pectoral Sandpipers, and Long-billed Dowitchers. The ecological importance of transients was greater than breeders in the lowland in the sense that food resources needed to support the transient population exceeded that needed to sustain the collective breeding effort. Density and diversity of shorebirds was much greater in a coastal salt-influenced habitat than any of the tundra plots, over the entire

season. Generalizing the above results, breeding bird density seems to be positively correlated with microhabitat diversity and wetness, while intense use by late summer migrants seems to be correlated with the presence of shallow ponds and very wet tundra.

Emergence of crane flies from terrestrial microhabitats and all insects from shallow water microhabitats was monitored in the three tundra plots. Cold weather in early to mid-July seems to have depressed emergence of adult insects at that time. Aquatic insects emerged in greater numbers when temperatures warmed on 23 July, but crane fly emergence did not increase. Reduced emergence of crane flies has been observed at Barrow, and a similar effect was probably responsible for very low emergence of Tipula at Canning River delta in 1980. Greatest emerged insect biomass was produced from aquatic sites, particularly polygon trough pond edges (thermokarst pools). Based on emergence of adult insects, food supply was greatest in the lowland plot, followed by the mesic and upland plots, in that order. This does not correspond to the ranking of the plots by breeding density (highest in mesic plot), although it does correspond to the ranking by total bird use. I hypothesize that in a warmer year the mesic plot would have produced far greater adult insect biomass because it contains much favorable habitat for Tipula.

Habitat selection by birds should be strongly influenced by the distribution of food resources only if food is in limited supply. The energetic value of the emerged insects in each plot was compared to the energetic needs of the shorebird chicks and the results indicated that food supply was insufficient to support reproduction at a level of 50%

fledging in 1980 on at least two of the plots. Therefore, the choice of a nesting site with ample available food resources for the young is not a trivial problem for tundra birds.

A correlation may exist between breeding bird density and microhabitat diversity, although more work is needed to evaluate this hypothesis. An ecological basis for this relationship would exist if breeding success were enhanced by the close proximity of dry microsites (for Tipula) and wet microsites (for aquatic insects, primarily midges). Availability of aquatic insects would be particularly important in a cold year such as 1980. The presence of polygon troughs should enhance the productivity of a habitat for birds because of the highly productive nature of these sites for insects.

The use of very wet tundra/shallow pond complexes by late summer migrants is probably related to the huge resource of midge larvae present in pond sediments. This resource is most available to birds when evaporation exposes the sediments of shallow ponds in mid- to late summer. The occurrence of midges with multi-year life cycles may be a factor in the late summer build-up of birds in suitable habitat along the Beaufort Sea coast.

Appendix. Results of plot censuses at Canning River delta, 1979-1980.

Lowland plot, 1979.

	26 JN	1 JL	6 JL	11 JL	17 JL	22 JL	27 JL	1 AU	9 AU	16 AU	24 AU	30 AU	Seasonal Mean	(S.D.)
Black-bellied Plover	0	0	0	0	0	11.1	0	11.1	14.8	3.7	29.6	55.5	10.5	(16.8)
Lesser Golden Plover	0	7.4	0	11.1	7.4	14.8	3.7	0	7.4	114.8	18.5	29.6	17.9	(31.7)
Whimbrel	0	0	18.5	0	3.7	0	0	0	0	0	0	0	1.9	(5.4)
Semipalmated Sandpiper	3.7	0	0	0	0	14.8	3.7	25.9	14.8	3.7	0	0	5.6	(8.4)
Pectoral Sandpiper	22.2	70.3	77.7	11.1	114.7	3.7	55.5	81.4	81.4	33.3	59.2	3.7	51.2	(36.0)
Dunlin	11.1	3.7	14.8	0	11.1	44.4	3.7	3.7	0	22.2	3.7	3.7	10.2	(12.6)
Stilt Sandpiper	0	0	0	0	0	0	0	0	11.1	0	0	0	0.9	(3.2)
Long-billed Dowitcher	0	0	0	0	0	0	0	0	14.8	107.3	107.3	0	19.1	(41.4)
Red-necked Phalarope	37.0	14.8	18.5	3.7	3.7	0	0	11.1	11.1	3.7	0	0	8.6	(11.0)
Red Phalarope	96.2	33.3	25.9	25.9	7.4	0	11.1	11.1	3.7	0	0	0	17.9	(27.3)
Unidentified shorebird	0	0	0	0	0	0	7.4	0	0	0	14.8	0	1.9	(4.6)
Lapland Longspur	25.9	33.3	33.3	29.6	18.5	33.3	18.5	62.9	29.6	85.1	99.9	29.6	41.6	(26.4)
All shorebirds	170.2	129.5	155.4	51.8	148.0	88.8	85.1	144.3	159.1	288.7	233.1	92.5	145.5	(65.9)
Total	196.1	162.8	188.7	81.4	166.5	122.1	103.6	207.2	188.7	373.8	333.0	122.1	187.2	(87.5)

Appendix. Continued. Lowland plot, 1980.

	6 JN	12 JN	18 JN	25 JN	1 JL	7 JL	13 JL	19 JL	27 JL	2 AU	8 AU	14 AU	20 AU	26 AU	Seasonal Mean	Seasonal (S.D.)
Willow Ptarmigan	0	3.7	0	7.4	0	0	0	0	0	0	0	0	0	0	0.8	(2.1)
Rock Ptarmigan	14.8	3.7	3.7	3.7	0	0	3.7	0	0	0	7.4	0	0	0	2.6	(4.3)
Black-bellied Plover	0	0	0	0	0	0	0	0	7.4	37.0	11.1	14.8	37.0	25.9	9.5	(14.0)
Lesser Golden-Plover	0	0	3.7	0	0	0	0	14.8	51.9	59.3	0	3.7	11.1	0	10.3	(19.8)
Ruddy Turnstone	0	0	0	0	0	0	0	0	0	3.7	0	0	0	0	0.3	(1.0)
Semipalmated Sandpiper	0	0	0	0	0	0	3.7	3.7	3.7	7.4	7.4	0	0	0	1.9	(2.8)
White-rumped Sandpiper	0	0	0	0	0	0	0	0	0	0	3.7	3.7	0	0	0.5	(1.3)
Pectoral Sandpiper	40.7	33.3	33.3	62.9	48.1	51.8	44.4	33.3	66.6	48.1	151.7	66.6	151.7	59.2	63.7	(39.1)
Dunlin	14.8	3.7	7.4	7.4	11.1	11.1	0	7.4	3.7	7.4	3.7	0	18.5	0	6.9	(5.6)
Stilt Sandpiper	0	3.7	0	0	0	0	3.7	0	0	0	11.1	0	0	0	1.3	(3.1)
Buff-breasted Sandpiper	0	0	0	0	0	0	0	0	0	0	7.4	3.7	0	0	0.8	(2.1)
Long-billed Dowitcher	0	0	0	0	0	0	0	0	0	0	0	0	62.9	29.6	6.6	(18.0)
Red-necked Phalarope	0	0	7.4	3.7	3.7	3.7	0	3.7	0	0	0	0	0	0	1.6	(2.4)
Red Phalarope	0	37.0	66.6	92.5	29.6	62.9	25.9	22.2	14.8	18.5	22.2	7.4	0	0	28.5	(27.8)
Lapland Longspur	55.5	37.0	48.1	59.2	77.7	66.6	74.0	14.8	144.3	22.2	55.5	85.1	59.2	3.7	57.4	34.6
All Shorebirds	55.5	77.7	118.4	166.5	92.5	129.5	77.7	85.1	148.1	181.4	218.3	99.9	281.2	114.7	131.9	(62.4)
Total	125.8	122.1	170.2	236.8	170.2	196.1	155.4	99.9	292.4	203.6	281.2	185.0	340.4	118.4	192	(72.6)

Appendix. Continued. Upland plot, 1979.

	23 JN	27 JN	2 JL	7 JL	12 JL	17 JL	25 JL	31 JL	9 AU	16 AU	23 AU	30 AU	Seasonal Mean	(S.D.)
Rock Ptarmigan	0	0	7.8	7.8	7.8	0	0	0	0	0	0	27.4	4.2	(8.0)
Lesser Golden-Plover	7.8	3.9	7.8	7.8	3.9	7.8	0	0	0	11.8	23.5	19.6	7.8	(7.5)
Whimbrel	0	0	3.9	0	0	0	0	0	0	0	0	0	0.3	(1.1)
Semipalmated Sandpiper	11.8	7.8	27.5	15.6	27.5	0	3.9	0	0	0	0	0	7.8	(10.6)
Baird's Sandpiper	3.9	0	0	0	0	0	0	0	0	0	0	0	0.3	(1.1)
Pectoral Sandpiper	0	11.8	7.8	0	15.7	0	3.9	35.3	27.5	23.5	7.8	0	11.1	(12.0)
Dunlin	3.9	7.8	3.9	3.9	23.5	0	0	0	0	0	0	0	3.6	(6.8)
Buff-breasted Sandpiper	15.6	19.6	39.2	0	23.5	3.9	0	3.9	35.2	3.9	0	0	12.1	(14.3)
Common Snipe	0	0	0	0	0	0	0	0	0	0	3.9	0	0.3	(1.1)
Red-necked Phalarope	11.8	7.8	11.8	0	0	0	0	0	0	0	0	0	2.6	(4.8)
Red Phalarope	7.8	7.8	0	0	3.9	0	0	0	0	0	0	0	1.6	(3.1)
Lapland Longspur	98.0	92.0	74.5	50.9	31.4	23.5	62.7	39.2	109.8	74.5	58.8	23.5	62.6	(29.1)
All shorebirds	62.6	66.5	102.2	27.3	98.0	11.7	7.8	39.2	62.7	39.2	35.2	19.6	47.7	(31.1)
Total	160.6	158.5	184.2	86.0	137.2	35.2	70.5	78.4	172.5	113.7	94.0	70.5	113.4	(48.1)

Appendix. Continued. Upland plot, 1980.

	6 JN	13 JN	19 JN	26 JN	3 JL	9 JL	15 JL	21 JL	27 JL	2 AU	8 AU	14 AU	20 AU	26 AU	Seasonal Mean	Seasonal (S.D.)
Rock Ptarmigan	3.9	3.9	3.9	15.7	0	0	0	0	0	0	7.8	54.9	0	0	6.4	(14.6)
Lesser Golden-Plover	0	3.9	0	0	0	0	11.8	0	0	31.4	0	0	66.6	0	8.12	(18.9)
Semipalmated Sandpiper	35.3	19.6	31.4	11.8	23.5	15.7	0	0	0	0	0	0	0	0	9.8	(13.0)
Baird's Sandpiper	7.8	3.9	0	0	0	0	0	3.9	0	0	0	0	0	0	1.1	(2.4)
Pectoral Sandpiper	27.4	0	11.8	11.8	3.9	3.9	7.8	0	0	23.5	3.9	27.4	19.6	15.7	11.2	(10.1)
Dunlin	7.8	11.8	3.9	3.9	3.9	0	0	0	0	7.8	0	3.9	0	0	3.1	3.8
Buff-breasted Sandpiper	15.7	7.8	27.4	3.9	0	0	3.9	0	0	0	0	3.9	0	0	4.5	8.0
Long-billed Dowitcher	0	0	0	0	0	0	0	0	0	0	0	0	0	7.6	0.5	(2.0)
Red Phalarope	0	7.8	7.8	7.8	7.8	3.9	3.9	3.9	0	0	0	0	3.9	0	3.3	(3.4)
Horned Lark	0	0	3.9	0	0	0	0	0	0	0	0	0	0	0	0.3	(1.0)
Yellow Wagtail	3.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	(1.0)
Lapland Longspur	94.1	78.4	94.1	110.0	137.2	74.5	70.6	39.2	82.3	227.4	62.7	58.8	109.8	15.7	89.6	50.0
Snow Bunting	3.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	(1.0)
All shorebirds	94.0	54.8	82.3	39.2	39.1	23.5	27.4	7.8	0	62.7	3.9	35.3	90.1	23.3	41.7	(31.1)
Total	199.8	137.1	184.2	164.9	176.3	98.0	98.0	47.0	82.3	290.1	74.4	148.9	199.9	39.0	138.6	(70.0)

Appendix. Continued. Mesic plot, 1980.

	8 JN	13 JN	20 JN	27JN	2 JL	8 JL	14 JL	20 JL	26 JL	31 JL	6 AU	12 AU	18 AU	24 AU	Seasonal Mean	(S.D.)
Willow Ptarmigan	0	0	3.9	0	0	0	15.7	15.7	0	0	11.8	0	0	0	3.4	(6.1)
Rock Ptarmigan	15.7	11.8	7.8	3.9	3.9	3.9	3.9	0	0	39.0	0	0	0	0	6.1	(10.7)
Lesser Golden-Plover	7.8	11.8	0	0	0	0	0	0	7.8	0	0	11.8	15.7	3.9	4.2	(5.6)
Semipalmated Sandpiper	35.3	31.4	47.0	27.5	23.5	23.5	3.9	0	23.5	0	7.8	0	0	0	16.0	(16.0)
White-rumped Sandpiper	0	0	0	0	0	0	0	0	0	0	3.9	3.9	0	0	0.6	(1.4)
Pectoral Sandpiper	0	27.5	47.0	66.7	549	47.1	19.6	35.3	39.2	47.1	70.6	15.7	27.5	23.5	37.2	(19.9)
Dunlin	7.8	15.7	15.7	11.8	19.6	7.8	3.9	0	27.5	7.8	31.4	0	0	0	10.6	(10.3)
Stilt Sandpiper	0	0	0	0	0	0	0	0	0	3.9	0	0	0	0	0.3	(1.0)
Buff-breated Sandpiper	0	15.7	3.9	7.8	3.9	3.9	0	3.9	0	0	3.9	0	0	0	3.1	(4.4)
Long-billed Dowitcher	0	0	0	0	0	0	0	0	3.9	7.8	0	0	0	0	0.8	(2.3)
Red-necked Phalarope	0	15.7	19.6	15.7	7.8	7.8	7.8	0	7.8	0	0	0	0	0	5.8	(7.0)
Red Phalarope	7.8	0	7.8	23.5	3.9	0	0	11.8	11.8	0	3.9	3.9	7.8	0	5.9	(6.7)
Lapland Longspur	105.9	105.9	117.6	156.9	129.4	101.9	101.9	78.43	180.4	82.4	266.7	51.0	43.1	11.8	109.5	(63.0)
All Shorebirds	58.7	117.8	141.0	153	113.6	90.1	35.2	50.97	121.5	66.6	121.5	35.3	51.0	27.4	84.5	(42.9)
Total	180.3	235.5	270.3	313.8	246.9	195.9	156.7	145.1	301.9	188.0	400.0	86.3	94.1	39.2	203.9	(98.6)

Appendix. Continued. West Branch flats plot, 1980.

	25 JN	27 JN	5 JL	8 JL	12 JL	19 JL	23 JL	27 JL	3 AU	7 AU	13 AU	22 AU	Seasonal Mean	(S.D.)
Rock Ptarmigan	0	0	0	0	0	0	0	0	0	20	0	0	1.7	(33.4)
Black-bellied Plover	0	0	10	0	0	5	0	0	20	15	0	50	8.3	(14.8)
Lesser Golden-Plover	15	45	10	50	55	10	65	5	5	5	0	10	22.9	(23.4)
Ruddy Turnstone	45	30	0	0	5	0	0	15	10	0	0	0	8.8	(14.0)
Red Knot	0	5	0	0	0	0	0	0	0	0	0	0	0.4	(1.4)
Semipalmated Sandpiper	75	275??	50	45	150	75	135	235	255	180	5	10	125.0	(94.7)
Western Sandpiper	0	0	0	0	0	0	0	0	0	0	0	70	5.8	(20.2)
White-rumped Sandpiper	0	0	0	0	10	0	0	0	0	0	60	0	1.2	(3.5)
Baird's Sandpiper	20	40	0	0	0	0	0	10	0	0	0	0	5.8	(12.4)
Pectoral Sandpiper	65	145	10	10	15	10	15	20	10	35	30	10	31.3	(39.3)
Dunlin	20	35	10	20	40	20	40	25	50	65	0	50	31.3	(18.7)
Stilt Sandpiper	0	0	0	20	0	15	35	0	0	35	0	45	12.5	(17.1)
Buff-breasted Sandpiper	0	0	0	0	0	0	0	0	0	0	0	5	0.4	(1.4)
Long-billed Dowitcher	0	0	0	0	0	0	0	0	0	0	0	40	3.2	(11.5)
Red-necked Phalarope	35	390	500	160	215	5	165	10	5	5	10	0	125	(169.3)
Red Phalarope	75	190	0	40	10	20	30	0	0	0	5	5	31.3	(54.8)
Unidentified shorebird	5	15	25	85	0	10	0	10	20	0	0	0	15.0	(23.5)
Lapland Longspur	0	10	10	5	5	35	40	80	125	30	20	15	31.3	(36.8)
All shorebirds	355	(1170??)	615	430	415	205	485	330	375	335	210	295	368.2	(118.5)
Total	355	(1180??)	625	435	500	205	525	410	500	385	230	310	407.3	(128.1)

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